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The Publications Committee of the Fiftieth Anniversary Celebration of the Ohio Academy of Science takes pleasure in presenting herewith the invitational addresses which were delivered before the Academy in Columbus during May, 1940, in connection with the golden anniversary. Twenty-eight papers were presented on that occasion, of which eighteen are published here. The remaining ten, because of previous commitments or for other reasons, are not to be published. It is hoped to be able to present in a later issue of the JOURNAL some of the historical data which were assembled for the occasion of the anniversary.

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PRESIDENTIAL ADDRESS

A PRESENT DAY EXAMINATION OF THE POSTULATES OF JOHN DALTON

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The constitution of the Ohio Academy of Science prescribes that on this occasion its President shall deliver an address. As much as I should like to confine my remarks to a discussion of some recent advances in the chemistry of the carbohydrates—an area of organic chemistry in which I find my greatest research satisfactions—a discussion of this special field of work on this occasion would have but a limited interest. However, there is one topic in which I am bold enough to believe that all members of the Academy have genuine interest. I refer to John Dalton's atomic theory of matter.

The concept of the discrete nature of matter has been one of the central themes of the science of chemistry since the first decade of the nineteenth century. In the middle nineties, the physicist became busily engaged with his brother chemist in a study of the nature of this small unit, in fact, a large share of his research endeavor is now directed toward the solution of this very fundamental problem. With the time at my disposal I shall attempt to make a brief examination of the postulates of John Dalton in the light of present day knowledge.

The atomic concept of matter finds its roots in philosophical thought that comes to us from remote antiquity. In an ancient Chinese document (Shoo King) it is conjectured that there are five elements, namely, water, fire, wood, metal, and earth. These elements were probably regarded as the materials from which all natural substances were derived, in quite the same way as we read today that the newly synthesized silk, nylon, can be made from air, water, and coal, which is true, but the actual process is a long journey. In the distant past, Kanada, the East Indian philosopher, gave utterance to the following opinion: "the mote which is seen in a sunbeam is the smallest perceptible quantity. Being a substance and an effect, it must be composed of what is less than itself. This again must be composed of what is smaller, and that smaller thing is an atom."

In the four or five centuries preceding the time of Christ, the Grecian philosophers gave much thought to this general problem. Leucippus (circa 500 B. C.) believed that all material substances were made up of atoms and empty spaces. His distinguished pupil, Democritus, reasoned as follows: "If every substance is divisible to infinity, and the division is never arrested, we come to one or two conclusions—*either nothing remains or something is always left.* From this reasoning he concluded that it was necessary to assume the existence of real, indivisible units of matter. This group of philosophers called themselves Atomists. Another school of Grecian philosophers under the influence of Aristotle maintained that matter was continuous and filled all space, a point of view that has had its adherents until relatively recent times.

The outstanding contribution in the pre-Christian era was the epic poem of Lucretius, "De Rerum Natura." In this poem Lucretius showed himself to be an ardent adherent of the atomic concept of matter, and by means of it he foreshadowed some of the fundamental notions underlying modern physics and chemistry. May I quote but one suggestive passage:

> "Infinite atoms in a boundless world,
> By endless motion build the frame of things."
> —Bk. I, 63, Johnson translation.

This and other examples of early philosophical inquiry should command our deepest admiration by reason of the general correctness of the views expressed concerning the nature of matter. Had the experimental method of verification of such ideas been in vogue at that time it is safe to assert that our present state of knowledge concerning Nature would have been much more advanced than it is at the present time.

Many important experimental discoveries were made in the latter decades of the 18th Century. From the laboratories of those fruitful years of scientific work came certain fundamental laws bearing upon the quantitative character of chemical reactions. We are indebted to Richter, the German, for the Law of Inter-proportionality, to Proust, the Frenchman, for the Law of Definite Composition, and to John Dalton, the Englishman, for the Law of Multiple Proportion. In an attempt to find a satisfying explanation for the quantitative relationships set forth in these three generalizations and that concerning the indestructibility of matter, John Dalton formulated the postulates which constitute his now well known atomic theory. The postulates of this important doctrine were these:

1. All bodies of sensible magnitude are constituted of a vast number of extremely small particles or atoms of matter bound together by a force of attraction which, as it endeavors to prevent their separation, is called attraction of cohesion; but as it collects them from a dispersed state is called attraction of aggregation or more simply affinity.
2. The ultimate particles of all homogeneous bodies are perfectly alike in weight, figure, etc. In other words, every particle of water is like every other particle of water; every particle of hydrogen is like every other particle of hydrogen, etc.
3. No new creation or destruction of matter is within the reach of chemical agency. All the elements we can produce consist in separating particles that are in a state of cohesion or combination and joining those that were previously at a distance.
4. The ultimate particles of all simple bodies are atoms incapable of further division. These atoms (at least viewed along with their atmospheres of heat) are all spheres and are possessed of particular weights which may be denoted by number.
5. If there are two bodies which are disposed to combine, then their combination takes place by atoms.
6. In an elastic gas each particle occupies the center of a comparatively large sphere and supports its dignity by keeping all the rest, which by their gravity or otherwise are disposed to encroach upon it, at a respectful distance.

In a discussion of these postulates it must be remembered that they were formulated in the earlier years of a period in which the answer to questions concerning man's physical surroundings were being sought by the laboratory method—a procedure that was destined to exercise a profound influence on the development of our civilization. In the first postulate Dalton was merely saying that all available quantitative experimental data concerning chemical reactions acquired fundamental significance if it were assumed that "all bodies of sensible magnitude are constituted of a vast number of extremely small particles or atoms," that is, matter behaves experimentally *as though* it were atomic, or granular in nature, as contrasted with the point of view that it is continuous in structure.

In support of this assertion the sciences of chemistry and physics of today furnish convincing experimental evidence. The laboratory records of chemistry reveal the existence of over a half million compounds, the vast majority of which have been synthesized by processes in which the existence of atoms was taken for granted. In no case do we find a departure in the composition of these compounds from that which could have been easily predicted, i. e., in no case do we find an exception to the laws of chemical combination upon which Dalton erected his theory. Throughout the world, the chemist, more especially the organic chemist, is constantly preparing pure compounds hitherto unknown. The foundation upon which the chemist's great success rests is the very spirit of that portion of postulate one which assumes the existence of atoms.

In the field of physics we find equally convincing laboratory evidence in support of the Daltonian doctrine with reference to the discrete nature of matter. I have chosen as illustrations the experimental determination of Avogadro's number (6.06×10^{23}), a physical constant which gives the number of molecules present in a gram molecular weight of any pure substance.

Jean Perrin, Professor of Physical Chemistry at the Sorbonne, found, in his classical study of the Brownian movement, that the value of Avogadro's Number was 6.82×10^{23} molecules. From a calculation based on the ratio of the mass to the electrical charge of the hydrogen ion, the value of this constant has been found to be 6.06×10^{23}, a value confirmed by Langmuir with his oil film technique. Again, on the basis of the volume of helium ion emitted from radium in one day, and also the number of such particles given off in one second, Rutherford and Boltwood calculated the value of this constant to be 6.16×10^{23}. Here we have four separate and entirely distinct methods of experimental approach to the determination of this important constant that yield data that are sufficiently in accord with one another to justify the spirit of postulate one, which to repeat assumes that matter is granular in its nature. Furthermore, it should be pointed out that the Avogadro Constant and the gram-molecular weight permit us to calculate the *actual* weight of any molecule, and from the result so obtained in the case of hydrogen we can determine the actual weight of an *atom* and that of the *electron*. The actual weight of the hydrogen atom was thus found to be 1.64×10^{-24} grams.

It may be added that were he living today Dalton would undoubtedly admit with the utmost satisfaction that 6.06×10^{23} molecules and

1.64×10^{-24} were numbers sufficiently large and sufficiently small respectively to justify and confirm his use of the phrase "a vast number of extremely small particles". Thus, it becomes evident that the modern physical sciences furnish what seems to be conclusive experimental data which justify the assumption of Dalton that matter is atomic in structure.

Since Dalton belonged to that group of natural philosophers who believed in the discontinuity of matter it was only natural for him to make the assumption in postulate four that "the ultimate particles of all simple bodies are incapable of further division—and are possessed of particular weights which may be denoted by number." What have our modern activities to say with reference to these assertions?

Concerning atoms having characteristic weight it should be noted that in 1905 John Dalton published the first atomic weight table. Among some of its features of interest to the chemist are these:

1. Hydrogen was used as a standard of comparison, and was assigned the value of 1, a procedure followed until relatively recent times. 2. An examination of the table shows that Dalton used the term "atom" to designate the smallest particle of both the present day element as well as the present day compound. 3. He arrived at the value for water, namely, 6.5, by adding his atomic weights of hydrogen and oxygen. The translation of these values into modern chemical symbols and formulas would give HO as the formula for water, i. e., one atom of each element. 4. Out of this table of atomic weights and the more accurate ones which followed it emerged a distinct effort to correlate these characteristic weights of the elements and their chemical properties. This is clearly shown in the publication of Doebereiner's idea of triad groups of elements in 1817, Newlands Law of Octaves in 1864, and the concept of periodicity amongst the properties of the elements as announced by Lothar Meyer in 1864 and by Mendeleeff in 1869.

In the eighteen-nineties, some ninety years after Dalton postulated that "the ultimate particles of all simple bodies are incapable of further division," three very important and apparently non-related discoveries were made. I refer to the discovery of radio activity and the element radium by Bequerel and the Curies, respectively; the discovery of the noble gases of the atmosphere by Ramsay and Rayleigh; and the discovery of X-rays by Roentgen. Today we know that these epoch making events are inextricably interwoven when they are considered in connection with the problem under discussion. We need only to be reminded that radium, thorium, and uranium are elements undergoing decomposition with an attendant evolution of three different rays, the alpha rays, or the He^{++}, beta-rays or the electrons, and the gamma rays, or X-rays of a very high frequency. The final product in each case was found to be the element, lead. Here then were atoms of certain known elements giving birth to the helium ion (He^{++}) an element of lower atomic weight, and to the age long known element, lead, truly a new kind of alchemy, and a case where elements were undergoing "further division" but not into like particles.

In his efforts to obtain more intimate knowledge concerning the nature of the atom, the present day physicist has attempted to shatter the atom into small particles through a vigorous bombardment. His

projectiles are the electron, the alpha particle, (or He^{++}), the proton, (or H^{+}), the recently discovered neutron, and deuteron, that is the ion of heavy hydrogen, (D^{+}). The heaviest piece of artillery is the modern cyclotron, an instrument which is capable of imparting a speed to these projectiles of the order of 9000–18000 miles per second with an energy of the order of 10,000,000 electron volts. Therefore, it is not a matter of great surprise that an occasional atom may be broken down into more simple particles when it is struck under these conditions.

Within recent months only the fission of uranium, the heaviest known atom, has been announced. This was accomplished by the bombardment of uranium with fast moving neutrons. Fourteen different elements were found in the atomic debris. (Ba, La, Ce, Kr, Rb, Sr, Y, Zr, Xe, Cs, Sb, Te, I, and Br.). By some authorities the fission of the uranium atom is regarded as the most important discovery of the year 1939, and it is also the greatest explosion in atomic history. With reference to that portion of postulate 4 which asserts that "the ultimate particles of all simple bodies are atoms incapable of further division," the modern physical sciences have shown that the fact of "further division" is a natural process as well as a laboratory one. However, this portion of the Daltonian doctrine which asserts that the atoms have characteristic weight which may be denoted by a number is in itself a great contribution to knowledge. It need only be remarked that all our analytical and synthetic processes in the field of chemistry whether they be academic or industrial rest upon these numbers which tell us the relative weight of each atom referred to some element chosen as a standard. Again we must not forget the stimulus which these numbers gave to a study of the possible relationship which might exist between these numbers and the chemical properties of their respective elements, thus leading to the discovery of the Periodic Law, which has pointed so unerringly to relationships and properties hitherto unperceived.

Again, we find Dalton referring to the property of weight in postulate two when he asserts that "The ultimate particles of all *homogeneous* bodies are perfectly alike in weight, figure, etc. In other words, every particle of water is like every other particle of water; every particle of hydrogen is like every other particle of hydrogen."

Some of the important present day facts bearing on the validity of postulate two are these: When the *atomic weights* of the specimens of lead obtained from the three radioactive sources mentioned above were determined by Theodore William Richards and others, a surprising fact came to light, namely, that the atomic weights of the lead obtained from these sources showed a variation from the classical value which was in excess of that due to experimental error. Here then we had experimental evidence for the existence of an element whose ultimate particles were not perfectly alike in weight. These atomic species of a given element are known today as isotopes, since a study of the various steps in the natural degradation of radium, thorium, and uranium show that these new kinds of lead atoms occupy the same position in the periodic arrangement of the elements. May we press this point further.

The discovery of deuterium, or heavy hydrogen, by Urey, Brickewedde and Murphy in 1932, was another event that had an important

bearing on the views of Dalton with respect to the homogenity of atoms. The atomic weight of heavy hydrogen (2.0147) is approximately twice that of ordinary hydrogen. (1.0078). The density of heavy water at 25° (1.1076) is approximately 11% greater than that of ordinary water (0.99707) at the same temperature (25°). Heavy water boils at 101.4° C. and freezes at 3.77° C. Since Giaque and Johnston found that oxygen existed as three isotopes then it follows that it is possible to have nine different molecules of water. (These would have the following formulas: H_2O', H_2O'', H_2O''', D_2O', D_2O'', D_2O''', HDO', HDO'', and HDO'''). This number may be increased in the future through the discovery of other isotopes of either hydrogen or oxygen.

Although our postulate asserts that "every particle of water is like every other particle of water, and every particle of hydrogen is like every other particle of hydrogen," your attention is invited to a fine example of clear and careful thinking on the part of John Dalton with respect to this one point. I will quote from his book entitled "A New System of Chemical Philosophy" published in 1808, volume I, page 142: "whether the ultimate particles of a body, such as water, are all alike, that is, of the same figure, weight, etc., is a question of some importance. From what is known, we have no reason to apprehend a diversity in these particulars; if it does exist in water, it must equally exist in the elements constituting water, hydrogen and oxygen. If some of the particles of water were heavier than others, if a parcel of the liquid on any occasion were constituted principally of these heavier particles, it must be supposed to affect the gravity of the mass, a circumstance not known. Similar observations may be made on other substances." This paragraph is one which clearly foreshadows the possible existence of isotopic elements, and the new compounds that might be formed from them.

These data with reference to the discovery of isotopic elements immediately raise the query concerning the significance of the chemist's atomic weight. It may be said at once that the chemist's atomic weights are the *average* weight of all the isotopic atoms composing a given element. Since the isotopes of any given element are generally chemically indistinguishable it is necessary to use *physical* methods for the determination of their respective atomic weights and the relative amounts of each species present. One of the most notable procedures for this purpose is that known as positive ray analysis, a fruitful method of research with which the names of Thomson, Aston, Dempster and Bainbridge are intimately associated. By this method it has been found that the atomic weights of the individual species are practically whole numbers, a fact which awakens a renewed interest in Prout's hypothesis. A comparison of the chemist's atomic weight of magnesium (24.32) with that determined by positive ray analysis (24.375) shows a difference of only 22 parts in 10,000. This remarkable concordance obtained by procedures as remotely different in the fields of chemistry and physics bears eloquent testimony to the sound thinking of the investigators to whom we are indebted for these experimental data.

With reference to the use of the word homogeneous in this postulate, John Dalton probably had in mind what we ourselves believed concerning the nature of an element and a compound prior to the "isotopian age." What was thought to be homogeneous we now know to be hetero-

geneous when regarded from the standpoint of weight and the various implications of weight. It must be remembered that the atoms of a given isotope are homogeneous, but the atoms of the several isotopic species are heterogeneous.

At this point reference must be made to that part of postulate 2 which asserts that "the ultimate particles of all homogeneous bodies are perfectly alike in . . . figure," and to that part of postulate 4, which declares that "*the atoms* of all simple bodies are spheres." Obviously, these statements have reference to shape and structure, a question that has occupied the attention of both the chemist and the physicist, regardless of whether the homogeneous bodies are elements or compounds. In this discussion we will confine ourselves to a brief review of the present day views concerning the structure of the atom. From the facts of the natural degradation of radioactive elements and the bombardment of atoms of various elements, we find that all elementary matter is associated with the following particles—some or all of which may be considered as the building stones of the atoms: (a) the *electron*, 1/1845 of the mass of the hydrogen atom and associated with a negative charge of electricity; (b) the *proton*, or the hydrogen ion, being a mass with a positive electrical charge; (c) the *neutron*, having a mass approximately that of the hydrogen atom but electrically neutral; (d) the *positron*, having the same mass as the electron but associated with a positive electrical charge; (e) the *mesotron*, a recently discovered particle of fleeting existence; (f) the *neutrino*, as yet of doubtful existence. At the present time we can hypothetically build atoms from the electron, the proton, and the neutron which will meet many of the specifications imposed by physics and chemistry of which the following are a few: these structures must account for the facts of periodicity in the properties of the elements; the facts of ionization; the valence theory; the existence of isotopic elements; the facts of radioactivity; and facts of spectroscopy.

As an illustration, may we discuss the existence of isotopic elements as related to their possible hypothetical structures. Our present point of view regards the atoms of ordinary or light hydrogen as consisting of a nuclear proton which bears one positive electrical charge, and one planetary electron with its one negative charge revolving about the positive nucleus at different energy levels. Physical theory tells us that if energy is absorbed by the atom, the electron moves to a higher energy level but if it falls to a lower energy level it emits energy. The energy so absorbed or emitted gives rise to absorption or emission spectra respectively. The quantity of energy so absorbed or emitted can be easily calculated from a knowledge of the light frequency and Planck's Constant or the quantum. For these ideas we are indebted chiefly to Rutherford, Bohr, and Sommerfeld.

Deuterium, or heavy hydrogen, is also regarded as having a nucleus consisting of one proton, and, in addition thereto one neutron, a particle that is electrically neutral; in other words, the nucleus of the heavy hydrogen atom is approximately (2.0186) double the weight of the ordinary, or the light hydrogen atom. Revolving about this nucleus also is one electron as in the case of the light hydrogen atom. Hence, we see that the electrical charge on the nuclei of both light and heavy hydrogen atoms is the same, i. e., one positive charge; and each of these

atoms has but one electron, i. e., one negative charge. From these two illustrations it is evident that within the nucleus resides practically all the mass of the atom since the mass of the electron in each case is negligible.

The fact that these two different atoms have the same nuclear charge but different nuclear mass is one of the first importance. In his now classical experiments, Moseley, in a study of the X-ray phenomena produced by the use of several different solid elements as targets in his apparatus found that the frequency of the emitted X-ray in each case was a function of the ordinal number of the element used. These ordinal numbers, i. e., hydrogen, 1, helium, 2, lithium, 3, and uranium, 92, are identical with the charge on the nucleus. They are called "atomic numbers." Out of this situation emerges the interesting fact that the isotopic species of a given element have the same atomic number regardless of the atomic weights of the several species. The composition of the three isotopes of magnesium to which reference has been made above is given in the following table:

	Particles Composing the Nucleus		Extra-Nuclear Particles	Number of Electrons in Energy Levels		
Symbol	Protons	Neutrons	Electrons	K-shell	L-shell	M-shell
$_{12}Mg^{24}$	12	12	12	2	8	2
$_{12}Mg^{25}$	12	13	12	2	8	2
$_{12}Mg^{26}$	12	14	12	2	8	2

The electrons are distributed about the nucleus at different energy levels or shells as shown in the above table. Since their number and distribution is the same in each case, it is clear why the chemical reactions of the isotopic species of a given element are generally identical.

We must now be reminded that recent discoveries have shown that the proton, neutron and the electron are not sufficient to account for the facts of radio-activity. This may be illustrated by the behavior of radio phosphorus whose formation and behavior are shown by the following reactions:

(a) $_{13}\text{Aluminum}^{27} + {}_{2}\text{Helium}^{4}\text{(ion)} \longrightarrow {}_{15}\text{Phosphorus}^{30}\text{(radio)} + {}_{0}\text{Neutron}^{1}$

(b) $_{15}\text{Phosphorus}^{30}\text{(radio)} \longrightarrow {}_{14}\text{Silicon}^{30} + {}_{1}\text{Positron}$

It is now believed that the positron is a manifestation of the binding or cementing energy which holds the nuclear portion of the radio-phosphorus atom together until the explosion occurs. Whether the mesotron, or meson, also functions as a cementing force cannot be definitely stated at this moment.

Thus far in our discussion of atomic structure we have confined ourselves to the use of building stones which were particles of definite magnitude. In 1924, de Broglie, the Frenchman, suggested that discrete particles, such as atoms, ions, and electrons should have wave properties as well as those of a corpuscular character, a point of view which reminds us of the discussion concerning the wave and corpuscular theories of light. This postulate was experimentally verified by Davisson and

Germer in the Research Laboratories of the Bell Telephone Company in 1927 when they found that a stream of electrons showed diffraction and interference phenomena when reflected from the surface of a crystal. In the following year (1928), G. B. Thomson obtained the same results when he projected a beam of electrons through a very thin gold film. Two years later (1930) Stern and Eastermann demonstrated that atoms of hydrogen and helium also have such wave properties in addition to those due to their corpuscular character. Out of the implications of these discoveries and the quantum mechanics emerged the powerful wave mechanics by means of which it was possible to determine the exact number of energy levels in the hydrogen atom and thus verify the assumptions which Bohr had made with reference to the spectrum of this element.

Since the atom has both corpuscular and wave properties it is evident that a mechanical structure alone is not sufficient to serve as a model of the atom—a particle which is so very complex in its properties.

In the beginning of our discussion it was stated that Dalton had formulated his theory in order to give significance to the laws of chemical combination and the law of indestructibility of matter. Since his theory advocated that matter was atomic in nature, the most natural conclusion for him to make was that the individual atoms themselves must also be indestructible. Hence, he asserts in postulate three that "No new creation or destruction of matter is within the reach of chemical agency." The spirit of this postulate has been one of the classical principles in the physical sciences. The following would be another expression of Dalton's thought. "Within the limits of experimental accuracy no change in the total mass can be detected as a result of any transformation which matter may undergo."

In 1906, Landolt performed a series of chemical experiments in sealed glass containers to test the validity of the law of conservation of mass and as a result he found that his experimental differences were of the order of only one part in ten million, i. e., a few hundredths of a milligram in 100 grams of reacting materials, a value so small that its significance could well have been disregarded.

Thanks to modern theoretical physics, the principle of the conversation of mass is merely one aspect of the principle of the conservation of energy, or, as Berthoud has so well expressed it, "matter and energy are not principles of different natures; they comprise a physical unity." This would imply that matter and energy are reversibly interconvertible. Einstein has expressed the relationship by his well known equation

$$E = mC^2$$

in which E is energy, m is the mass, and C is the velocity of light. This equation means that "an increase in the energy of a body means an increase in its mass, and that every form of energy has an equivalent mass." Kaufmann, a German worker, seems to have furnished experimental evidence for these relationships when he found that an increase in the velocity of an electron produced an increase in its mass.

By the use of Einstein's equation, it can be shown that the energy evolved in the formation of one gram molecular weight of water from its elements has a mass of 3 millionths of a milligram. When compared to

the 18 grams of reacting materials this seems to be a very small quantity, but it is none the less a very real one (3×10^{12} ergs).

Thus it becomes clear that there must be an increase in mass in all endothermic chemical changes in quite the same manner as there must be a diminution of mass in all exothermic chemical changes.

The contribution of present day workers in the physical sciences has greatly enlarged the meaning of the relationship which Dalton enunciated in this postulate. Today as well as in Dalton's time the fundamental character of this great generalization remains unchanged, i. e., we are only becoming aware of its comprehensive character.

Our natural philosopher was also concerned with the mechanism of chemical reactions as is evidenced by postulate five wherein it is stated that "if two bodies are disposed to combine, then their combination takes place by atoms." The chemist has always been interested in knowing the number of atoms of one element which will unite with a definite number of atoms of another element, an inquiry out of which the theory of valence was born. Today we believe that the electronic section of the atom, i. e., the extra nuclear part, is the one that functions in chemical reactions, that is, that the forces to which John Dalton referred are electrical in their nature. This is equivalent to saying that today we regard the valence concept to be an electronic one. If this is true and our present picture of the orientation of the electrons about the nucleus is correct, we have reason to expect a number of different electronic mechanisms whereby chemical union would take place to form at least three types of compounds whose existence are realized in the following classes:

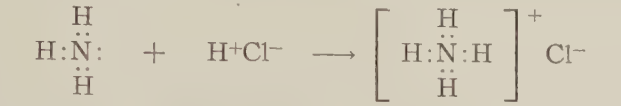
1. *Electrovalent Compounds:* These compounds are formed by the transfer of electrons from the metallic to the non-metallic element, an action which yields a positive ion and a negative one. These changes may be represented by the union of a sodium atom to a chlorine atom to form sodium chloride, a reaction in which the chlorine atom acquires an electron from the sodium atom thus leaving the sodium with a positive electrical charge and the chlorine with a negative charge. These charged particles are called ions. An X-ray examination of solid sodium chloride confirms the view that the crystal of this compound contains the ions of its components and not its atoms.

2. *Covalent Compounds:* The covalent compounds are formed by a mutual sharing of electrons of the elements composing the new substance, a point of view which should be credited to G. N. Lewis, of the University of California. In general, the chemical bond thus formed consists of two electrons, one each having been contributed by two individual atoms. The bond thus formed is usually equivalent to the single bond of an organic compound. This electronic concept of shared electrons may be represented by the marsh gas molecule as follows:

$$4\mathrm{H}\cdot + \cdot\dot{\underset{\cdot}{\mathrm{C}}}\cdot \longrightarrow \mathrm{H}:\dot{\underset{\cdot\cdot}{\overset{\cdot\cdot}{\mathrm{C}}}}:\mathrm{H}$$
$$\mathrm{H}$$

It should be pointed out that the theoretical physicists, Heitler and London, in their studies of the nature of valence assumed that the electron pairs which give rise to a covalent bond must be of opposite spin.

3. *Coordination Compounds.* In coordination compounds the "two electron valence bond" is furnished by a single atom which in turn may unite with another atom in order to bring the outer shell of the second atom up to eight or more electrons. The following is a familiar illustration:



Ammonia + Hydrochloric Acid ⟶ Amonium Chloride

The bond here consists in the nitrogen having a "lone pair" of electrons, or a duplet available for the hydrogen ion. Thus we see that the modern conception of the structure of the atom furnishes us a satisfying mechanism whereby chemical combination takes place between atoms as was postulated by Dalton. Furthermore, we have been able to classify many compounds into groups by reason of the electronic mechanism whereby chemical union takes place.

Postulate VI. The sixth and last postulate assumes that "in an elastic gas each particle occupies the center of a comparatively large sphere and supports its dignity by keeping all the rest, which by their gravity or otherwise are disposed to encroach upon it, at a respectful distance." This quaint statement is easily recognized as the now universally accepted kinetic-molecular theory of matter. It is said that the kinetic concept involved in this postulate comes to us from Daniel Bernouilli, a Swiss mathematical physicist, who, in 1738, developed a kinetic theory of gases.

That Dalton was correct with reference to his statement concerning each molecule occupying "the center of a comparatively large sphere" is evident from the fact that the space between the molecules composing steam at 100° is 99.94% of the total volume, i. e., the actual molecules of steam occupy only .06% of the total volume, i. e., only 6 cc. in 10,000 cc.

This postulate also tells us of the unceasing motion of gaseous particles. One of the most convincing pieces of evidence of molecular motion is the Brownian movement. As a result of Perrin's work referred to above on the Brownian movement in emulsions, Ostwald, *one* of the early German workers in physical chemistry, was moved to say that "the agreements of the Brownian movement with the requirements of the kinetic hypothesis justify the most cautious scientist in now speaking of the experimental proof of the atomic theory of matter." In this connection it only is necessary to refer to the great contribution made to the science of chemistry and physics by the kinetic molecular approach to a vast number of well known chemical and physical phenomena.

Finally, in the light of present day knowledge, we arrive at the following conclusions in evaluating the postulates of John Dalton enunciated one hundred and thirty-five years ago.

1. Modern physics and chemistry furnish convincing laboratory evidence for the existence of atoms as John Dalton set forth in his theory.

2. The degradation of these atoms into other particles is a natural as well as a laboratory process.

3. The atoms of a given element are not homogeneous as Dalton

believed, but they are found to possess different masses. These different species are known as isotopes.

4. Atoms consist of the following corpuscular particles, the electron, the proton, the neutron, the positron, the mesotron (meson), and possibly the neutrino.

5. Atoms have wave properties as well as those properties arising from their corpuscular character.

6. The atoms consist of a nucleus made up of protons and neutrons while the extra-nuclear portion of the atoms consists of electrons. The isotopes of a given element are due to the variable number of neutrons.

7. The spirit of Dalton's view that no new creation of matter is within the reach of chemical agency has been greatly enlarged in its meaning.

8. Dalton's view that chemical combination takes place by atoms has been greatly enriched by our present electronic conception of valence.

9. Dalton's Kinetic picture of the atoms has in no wise been changed.

The purpose of this discussion has been to trace in brief outline the life history of one of the basic theories underlying so much that is fundamental in the fields of knowledge represented in this Academy. It would seem that the enlargement of the points of view in certain of these postulates and other changes which have been made by reason of later experimental and theoretical considerations would be fairly typical of the philosophical process which aids us in a better understanding of the surroundings in which we find ourselves as human beings. In closing may I quote from the dedication inscribed by Charles Daubeny in his book entitled "Atomic Theory"—published in its second edition in 1850—a dedication by an academician who had an appreciation of the scholarship of John Dalton.

TO

THE MEMORY OF
JOHN DALTON, F. R. S.

Late President of the Literary and Philosophical Society of Manchester,
Corresponding Member of the Academy of Sciences of the Royal Institute of France, and Honorary, D. C. L. of the University of Oxford,

THE FRAMER OF A THEORY
WITH RESPECT TO THE MODE OF COMBINATION BETWEEN BODIES,
WHICH STANDS FOREMOST AMONG THE DISCOVERIES OF THE PRESENT AGE,
FOR THE UNIVERSALITY OF ITS APPLICATIONS,
AND THE IMPORTANCE OF ITS PRACTICAL RESULTS;
HOLDING THE SAME KIND OF RELATION TO THE SCIENCE OF CHEMISTRY,
WHICH THE NEWTONIAN SYSTEM DOES TO THAT OF MECHANICS:
AND THROWING LIGHT,
NOT ONLY UPON ALL THE ORDINARY SUBJECTS OF CHEMICAL INVESTIGATION,
BUT EVEN UPON THOSE MORE SPECULATIVE QUESTIONS
WITH RESPECT TO THE CONSTITUTION OF MATTER,
WHICH SEEMED TO LIE BEYOND THE REACH OF EXPERIMENTAL INQUIRY.

RESEARCH ON THE CENTRAL AUDITORY MECHANISMS: SOME RECENT METHODS AND RESULTS[1]

E. A. CULLER,
University of Rochester

Whenever I speak upon the topic of hearing, I am reminded of an incident which occurred some years ago at a meeting of the National Academy of Science. A young man from one of our large universities had just reported a study in audition. As he concluded, Dr. Cattell arose—dean of American psychology and Nestor of American science. His first comment was to this effect: "Whenever you think you've discovered something new about hearing, turn to Helmholtz and you'll find it there." This tribute to the greatest experimental theorist in the history of acoustic research was indeed well deserved; but it was considerably more true when spoken fifteen years ago, than it is today. We now know some things about hearing that even Helmholtz, with his unrivaled insight, did not perceive.

This new knowledge is due, in large part, to new methodology. I need not remind you that the milestones in scientific progress are marked by new methods of research. Emphasis upon methodology is a cardinal distinction between the man in the laboratory and the man on the street. Whenever I speak to laymen about our work, I am often reminded by my hearer that he is not interested in methodology; what he wants are facts. He makes the statement with something of an air, as though he prided himself on being hard-headed and practical. But we all know, if we know anything about science, that the observations we get are a function of the methods we employ; that facts are the fruit of operations. For that reason let us begin with a few methods that are basic in auditory research as a means to understanding some of the facts which I wish to report.

The first method historically was doubtless *clinical*. If everybody had perfect and uniform hearing from birth until death, never suffering any impairment because of accident or disease, it is doubtful that hearing would ever have been a problem. Because some of us hear better than others, because we hear better early in life than later, because hearing may be completely destroyed through some injury, we are forced to think about the mechanisms of hearing—how they operate and what can be done to restore them. In other words, the accidents of Nature prod man to research. In this sense, Nature may be called the first experimenter. One of the great contributions of Darwinian theory is its revelation that the world we inhabit is an experimental instead of a static universe. In the clinical method Nature sets the

[1]Communication No. 37 from the Laboratory of Physiological Psychology (Animal Hearing), which was transferred from the University of Illinois to the University of Rochester in 1938. This laboratory is maintained with aid from the Research Council, American Otological Society.

problem and man tries to solve it. A patient whose hearing disturbs him appears in the consulting room of an otologist; who thereupon, in addition to other tests, plots a complete audiogram of each ear. He thus determines as well as possible the locus and nature of the malady. Ofttimes little can be done beyond prescribing a hearing-aid. The patient is then examined year by year to note what changes occur and finally, if the physician lives long enough and the patient dies soon enough, the ears which have been so often tested are removed and sectioned in order to correlate their anatomical deficiency with the functional hearing-loss. The procedure is sound but has several great defects. 1. It is insufferably slow. The patient may live longer than the physician; so that the answer to a simple question of fact may require several generations of careful work by many investigators. 2. But a still graver difficulty is that Nature, although the first experimenter, is unquestionably one of the poorest. A young man of the laboratory, who could not plan his experiment better than Nature does, would find it hard to win even a bachelor's degree. A clinical lesion usually implicates so many separable factors in the ear that it is quite impossible to say which one is responsilbe for the hearing-loss. At Johns Hopkins Medical School is located one of the world's most extensive collections of sectioned human ears, together with audiograms showing the functional condition of each one. This vast body of material has accumulated over many decades and represents a huge expenditure of time, energy, and money; yet I venture to say that we can learn more by the use of modern experimental techniques in six months from a cageful of guinea pigs about localization of function in the cochlea than we can from this great assemblage of clinical evidence. While the clinical method will never be superseded, its deficiencies are such that little real progress could be made until adequate *experimental* methods were devised.

Of these experimental methods, the first to consider is *conditioning*. This term is familiar to you. It was bestowed by the Russian physiologist Pavlov and is illustrated in one form by the familiar laboratory picture in which a dog stands with one foot resting upon a metal grid which can be charged with a small electric potential. If you sound a tone about two seconds before the paw is stimulated, the animal will soon begin replying to the tone by withdrawing his foot from the grid. We say that he has been "conditioned" and now reacts to the sound as he formerly did to the shock. After conditioning has been established, the tone is made weaker and weaker. The animal continues to react as before until at last he begins to falter, responding sometimes but not always. With continued reduction of intensity, a point is eventually reached where no response occurs at all: this implies that the tone is now completely inaudible. This simple procedure has proved extraordinarily fruitful in studying problems of hearing. The older experimenters, who tried to get away from the limitations of the clinic, were impaled upon one horn of a dilemma. If they worked with human patients, they could test the subjects's hearing but they could not operate surgically on him. After all, we can't drill a hole in our neighbor's ear to see how that would affect his hearing. If, however, they

tried to use animals, they could indeed operate on the subject but they were unable to measure what it *could* and *could not* hear. Until very recent times, effective laboratory research on hearing was blocked by this dilemma. Now, however, by the conditioning procedure we can train a dog or cat or guinea pig to react visibly to every sound it can hear, however faint, and thereupon measure its audiogram. We can then anesthetize the animal and make some well defined lesion in the acoustic tracts. As soon as the animal recovers from anesthesia, it will tell us by its reactions the exact effect of our lesion. By making comparative tests on our trained animals and on ourselves, we have proved that a test-animal is fully as reliable a witness as a good human patient. Almost every problem that arises in the otological clinic with human beings can now be tested with experimental controls in the animal laboratory.

Another experimental method which has proved of the greatest value in recent years is *electrical*. It has long been known that the activity of living cells is often attended by electric phenomena. So well was this understood even fifty years ago that these electric potentials were designated "signs of life." One could, for example, distinguish a living seed from a dead one by means of the minute electric currents generated by the former. There are, of course, other signs of life. A living cell will give off CO_2 at all times; an active cell will emit more CO_2 than a cell which is resting. This has been well demonstrated by an instrument known as the biometer or "life meter," which reveals that an active nerve fiber gives off fully twice as much carbon dioxide as the same fiber when at rest. Likewise living cells when active emit heat; even the minute nerve-cells generate small quantities of heat when they are conducting impulses. The peculiar advantage of electrical procedure is, however, that living cells can be studied *in situ* more readily than by any other means. Electric techniques are so highly developed that we can put an electrode against the inner ear or the auditory nerve, pick up the minute potentials therein generated, lead them through an amplifier into an oscillograph, and study their properties. The contribution of this method to understanding the function of the ear and its associated tracts is hard to overstate. What we may call the modern period of auditory investigation begins with the application of electric methods to the study of the cochlea and the cochlear nerve.

In many cases the two experimental methods, electric and conditioning, are applicable to the same problem. When used in combination, they constitute an extremely powerful tool for the study of acoustic mechanisms.

In recent years research by use of these methods has been principally of two kinds. 1. Some investigators have continued to study the activity of the cochlea in different animal-forms and to seek an adequate description of the peripheral structures and operations by which a sound-wave is converted into discrete nerve-impulses. 2. Others have examined the structural characteristics and functional problems of the neural conduction-system in its course from cochlea to cortex; the purpose of these studies being to describe and evaluate the neural events which unite the functional levels of the acoustic system.

It may be well to remind you that both the cochlea of the inner ear and the neural components of the acoustic system emit electric potentials when sound vibrations are impressed upon the ear. These two types of potential, however, differ in certain important respects. 1. Synchronized cochlear potentials can be detected as high as 6000 cycles or more whereas synchronized neural potentials seldom are reported beyond 2500 or 3000 cycles. 2. The cochlear potential usually resembles (apart from aural distortion) the wave form of the impressed sound, whereas the neural potentials look like similar potentials in other sensory nerves, being essentially monophasic and negative. 3. The cochlear voltages are many times as large as the neural, with the result that they spread by ordinary electric transmission to points several centimeters away from their origin. The neural potentials being much feebler can usually be detected only in close proximity to the nerve-cell which generates them. 4. Cochlear electrophonics, which thus spread in all directions by ordinary transmission, travel at considerably higher velocity than do neural impulses which propagate at the usual speed of nerve-impulses (e. g., 30 meters per second). 5. Cochlear potentials effectively resist narcosis whereas neural potentials are appreciably reduced by most anesthetics. 6. Cochlear potentials may persist for minutes or even hours after demise of the animal, though with reduced intensity, whereas the neural potentials commonly disappear at or just prior to death.

In accord with the original plan of this symposium, I shall confine myself principally to reporting some studies bearing upon the phenomena that occur in the neural acoustic system central to the cochlea; that is, studies which belong to the second group of investigations just mentioned.

1. I shall first notice a study now in progress by W. D. Neff of our laboratory on the effects upon hearing in the cat of partial section of the eighth nerve. Changes in sensitivity occasioned by local damage to the eighth nerve, which connects the cochlea to the brain stem, are observed by the conditioned-response technique. The cat is first conditioned until it responds clearly to any audible sound. The audiogram of the animal is then measured at the various octave frequencies from 125 cycles to 8000 cycles and, in some cases, for two additional octaves (62 cycles and 15000 cycles). When the animal's normal hearing is thus determined, the cochlea of one ear is destroyed so that all auditory impulses must pass to the brain via the nerve that is later to be partially sectioned. Destruction of the single cochlea results in surprisingly small loss of total sensitivity, usually about two or three decibels. (A decibel is the standard unit in acoustic measurements and is, very roughly, that difference in physical intensity of two tones which can just be perceived by a normal ear). As soon as the animal's thresholds for the several frequencies have been determined for the one remaining ear, the second and critical operation ensues. Under complete narcosis the eighth nerve of the intact ear is carefully exposed. The nerve tissue being quite soft can be removed in any desired amount by a suction-pipette so that part of the nerve is left intact but the remaining fibers are effectively interrupted. After the animal is sufficiently recovered

for testing, the postoperative limens are secured. Comparison of these limens with those which preceded the operation will, obviously, reveal the losses due to partial section of the nerve. Results to date reveal that a very small lesion brings no significant loss at any frequency, whereas with larger lesions, marked losses appear at several of the higher frequencies. Since the experiment is not yet complete and histological evidence is not yet available, interpretation must be tentative; but several conclusions are already obvious. First, not all fibers of the eighth nerve need be severed to render an animal deaf to certain frequencies. Secondly, the remaining intact fibers give at other frequencies the same sensitivity (limen) as did the whole nerve.

2. A second study was performed by Ades and his collaborators at the level of the medial geniculate bodies in the cat. These two nuclei, right and left, being the final way-station from cochlea to cortex, provide an ideal site for determining in what manner cochlear impulses are transmitted to the brain. The general procedure was as follows: The intact cat is first conditioned and its normal audiogram obtained for an adequate sample of the audible range (octave frequencies from 125 to 8000 cycles). Localized electrolytic lesions are then effected at corresponding points of the two medial geniculates. The cat is then retested to determine what losses, if any, have occurred in its hearing. Finally, the animal is dispatched and the brain prepared and examined by histologic methods.

Inspection of the audiograms shows that localized lesions in symmetrical areas of the two geniculates result in some attenuation of auditory sensitivity for all frequencies tested, but that the degree of impairment differs widely. The variation is not haphazard but in every case conforms to a definite pattern, the loss being greatest at one or two frequencies, graduating down to a minimum at those most distant from the focal frequencies. Cats with lesions in corresponding areas display a similar distribution of hearing losses. Loci for the several frequencies seem to be as follows: 8000 cycles, dorsal region; 4000, anterior; 2000, lateral; 1000, posterior; 500, medial. The lower frequencies, 250 and 125 cycles, were in no case attenuated to maximal degree, but apparently traverse the ventral side. The several loci thus appear to follow a linear course, beginning with higher frequencies in the dorsal section and circling downward to the ventral region where the lower frequencies appear.

3. The medial geniculate nucleus in the cat has also been explored by Coakley, using an entirely different method. If there is a spatial distribution of fibers within the nucleus, it should be possible to determine their position by recording the electric potentials generated in any given case by the active units. Accordingly, the distribution of potentials in the nucleus has been studied for five frequencies of stimulation arranged in octave steps from 125 to 2000 cycles. Since the potentials above 3000 cycles became so feeble as to be practically imperceptible, our data are limited to frequencies below that point. The potentials generated by an impressed tone were measured at about 120 points arranged uniformly throughout the nucleus and just beyond its margins. Of course only a small number of points could be studied in any one

animal but each point was examined in about six cats. Summarizing the results for all animals, we find that for each frequency applied to the ear, the potentials are maximal for amplitude in one region and become smaller as the needle is moved in *any* direction from this area. If these maxima are arranged in order of frequency, they constitute a figure similar to a conical helix. Further analysis of the data reveals the approximate course followed by each group of fibers. In addition exact synchronization between impressed frequency and neural pulses in the nucleus was observed up to 2500 cycles. This implies that, whatever number of negative (or positive) pulses is generated in the cochlea, the same number will still be found (up to 2500 cycles) in the neural action-currents of the medial geniculate.

4. E. A. Lipman has accumulated some material on cortical function in hearing. The procedure is similar to some already mentioned. The normal audiogram of a trained dog is first measured at the usual representative frequencies (125 to 8000 cycles). The entire temporal (acoustic) area of one side of the cortex is then removed and the animal's audiogram again tested. Even though only one side of the brain is now intact, hearing-losses are quite negligible, being in no case more than three or four decibels. The second and critical operation then follows in which a small localized part of the remaining intact side is removed with the suction-pipette. Postoperative tests again reveal what losses, if any, occur at each frequency.

In general the losses at a specific frequency are not large, about 10 decibels, but the results to date indicate that hearing losses are confined to the area comprised by the medial and posterior ectosylvian gyrus and the adjacent medial and posterior sylvian gyrus. Removal of cortex beyond this area seems to have no effect upon hearing. Thus far lesions in the ectosylvian gyrus are followed by losses at 500 cycles and below, whereas lesions in the adjacent sylvian area seem to bring losses at higher frequencies from 1000 cycles up. These results indicate that focalization of responses is not so sharp as elsewhere but still present. The exact locus for each of the several frequencies awaits further tests.

From these and other observations we may infer that different tonal frequencies, when impressed on the ear, actuate different areas or patterns of receptive cells within the cochlea and that the impulses thus generated traverse differential pathways to the auditory projection center of the cortex; but that the number of pulses per second passing to the cortex rises in step with the impressed tone, and thus provides a second clue by which the organism can perceive pitch. The *relative* contribution of these two factors (spatial and temporal) must await further analysis.

SOME SOCIAL ASPECTS OF DEAFNESS

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Helen Keller once said: "I am just as deaf as I am blind. The problems of deafness are deeper and more complex, if not more important, than those of blindness. Deafness is a much worse misfortune. For it means the loss of the most vital stimulus—the sound of the voice that brings language, sets thoughts astir, and keeps us in the intellectual company of man."(1)

There is considerable truth in these few lines. Deafness strikes deep in the social roots of the individual who is so handicapped.

It is the purpose of this paper to present to you briefly some of the social aspects of deafness; this is with particular reference to the deaf as distinguished from the hard-of-hearing. To differentiate between these, the hard-of-hearing are those in whom the sense of hearing, although defective, is functional with or without a hearing aid; the deaf are those in whom the sense of hearing is nonfunctional for the ordinary purposes of life. The term "deaf and dumb" is no longer used as too frequently it implies stupidity which is not true of the group. Neither is the term deaf-mute an acceptable designation. The child who has been deaf from an early age does not speak because his deafness prevents the acquisition of speech in the normal imitative manner. Organically his organs of speech are normal. Deaf babies cry, coo, and babble, much as other babies do. While the average deaf child can be taught speech, he does not acquire it unless he is given special instruction.

Deafness not only acts as a barrier to speech but blights the child's language. The little hearing child hears words repeated scores of times and early begins to link these words to objects or actions. In place of language a system of crude gestures is built up for the deaf child. These are necessary for the child to make his wants known. The means of communication is so limited that it seriously retards his progress. Explanations are difficult to make and are seldom or inadequately made. Parents finding that they cannot reason with the child or make explanations, give him what he wants. Of course if he doesn't get it, he frequently resorts to tantrums. The gestures used generally relate to the child and not to others. This tends to make his world a self-centered one, with little consideration for others.

While some parents indulge their deaf children as far as they possibly can, others err in the other extreme by punishing them for misbehavior that resulted from a lack of understanding on the part of the child.

It is apparent that little deaf children must experience a feeling of frustration in not being able to express themselves or inquire into the how, what, who and why of the world about them.

Such characteristics have been commented on by others. I refer you to Brunschwig, "A Study of Some Personality Aspects of Deaf Children,"(2) and also Ewing and Ewing "The Handicap of Deafness."(3)

It is perhaps worthy of mention here of the weary and often painful rounds on which these children are taken in the hope that their hearing will be restored. Frequently after the family physician has attended them for some time they are referred to an otologist. Though the otologist may tell the parents that the child is irrevocably deaf they continue to go from doctor to doctor, to charlatan and quack, administering pills, salves and worthless nostrums. Two or three years ago we had a boy return to school with a box full of pills to restore his hearing. There were seven different kinds of pills in the box, and he was to take one of each after each meal. While faith cures are not to be regarded as painful experiences, it is not uncommon to have children kept out of school for long periods of time awaiting such cures to take effect.

Unfortunately most parents do not require what they reasonably could of their small deaf children. Swayed by sentiment, they think of them as poor little deaf children who are unable to do anything for themselves. A year ago we had a six-year-old boy enter school whose grandmother still gave him his milk in a nursing bottle. While this is unusual it shows the extent to which "babying" can be carried. Each year we find that a large proportion of our beginning children can neither feed nor dress themselves properly, yet they could easily have been taught these things had their parents approached these problems sensibly. Through a lack of understanding, and proper handling, behavior problems appear and grow unchecked. The mother of one of our small boys, who caused his parents no end of annoyance and despair, told me that she had taken the child to a well known surgeon, and asked him to open up the boy's head to see what made him so mean. At school—after he has settled down from a home visit—he is a nice little fellow.

Paralleling a statement by Druschba (4), it is as true of deaf children as it is of hearing, that they are neither good nor bad originally. The character and behavior problems that arise, come not from their deafness, but from faulty or ineffectual methods of training. It is pertinent to observe at this point that little deaf children whose parents are deaf are quite generally more normal, both in behavior and achievement, than deaf children from hearing families.

When the deaf child reaches school age he comes to another social turning point. Occasionally such children are not sent to school at all; more frequently the parents delay sending them for two, three, or more years. In 1937 we admitted a girl who was then twenty years of age. The girl appeared to be of good mentality but her mother had simply kept her at home. It was on the insistence of a sister that she was finally brought to school. She could not answer such simple written questions as "How old are you?" and "Where do you live?" This girl is now doing work on the level of pupils who have been in school six years and the outlook in her case is good. Sometime ago I received a letter from a woman concerning her deaf sister who was then forty years old. The mother had taken care of her during her lifetime. After the death of the mother, the deaf woman lived with her sister. The letter stated that while she was quite intelligent, she was unable to read or

write. It was evident that she was proving to be an unhappy burden on the family. Of course this woman was beyond the reach of our school. While these are exceptional cases, they show how dependent the deaf are on proper instruction.

Today practically all educable deaf children are sent to some school. It is true that some of them are to be found in the class rooms of regular public schools. This comes about because the parents are either unaware of facilities for special instruction or because they are unwilling to let them go away to school. Through a lack of discernment or indifference on the part of public school authorities they are allowed to remain. Sometimes intelligent deaf children are kept in these classes and both regarded and treated as feeble-minded. Socially their deafness isolates them from other children. Usually their hearing schoolmates ignore them, occasionally they are teased or made the butt of practical jokes. If they remain in a school for the hearing for any length of time, it is a common practice to push them on every year or two without regard to educational achievement. In the last few years several children have come to our State School after having an experience of the type described. One girl, whose father was a member of the local board of education, had been promoted year after year until she reached the eighth grade where she was failed by a teacher who had just come into that school system. The father had had some misgivings over the school promotions of his daughter. These misgivings were not without foundation; we found that the girl's educational level was around the second grade. Socially and educationally maladjusted, children of this type enter our schools for the deaf, literally broken in spirit and with a defeated outlook on life. While there is a sufficient number of these children to justify mention, the percentage of them is small. Most deaf children enter schools for the deaf without long delays.

For the little child who is profoundly deaf there are two principal means of instruction; he may be instructed either orally, or he may be instructed manually. Each of these approaches has its shortcomings as well as its advantages. The social aspects of both are such that they should be discussed here.

The oral approach consists of teaching the child speech and speech-reading (or lip-reading as it is frequently called) and also using this means of communication in regular class-room activities. To appreciate what this involves it is necessary to know something of the procedure.

Speech instruction begins with the teaching of the elementary English sounds, the consonants and the vowels. Some of these are easily taught, others are much more difficult. One of the first consonants taught is H, which is simply an expulsion of the breath through the open glottis. The child readily learns this sound by imitation. Usually the first vowel taught is Italian A or AH. In producing this sound no modification by the lips is necessary; the tongue remains flat in the mouth. Contrary to popular belief, it is not difficult to get voice from a deaf child. Usually they understand by watching the teacher and feeling the vibration in her throat. However the quality of the voice is another matter. The child, not hearing the sound he is producing, may give it in an unnatural and displeasing voice. Considerable

effort is made to obtain a good quality of voice in teaching the first vowel. The development of other vowels and consonants is more difficult, the formation of some of them being quite complex. These are taught in a variety of ways, such as comparing or contrasting them with sounds already learned; by manipulating the child's tongue; or drawing diagrams showing the required position of the tongue and other vocal organs. The child is taught to put these sounds together to form words, to syllabify words and accent them, and to phrase sentences.

The companion of speech is speech-reading. This is developed from a simple beginning. The child is shown some small toys such as a ball, a fish, and a car. The names of these present a dissimilar appearance on the lips and the average child is soon able to select the proper toy by watching the teacher's lips. Speech-reading is gradually extended to include familiar objects and actions. The level of attainment sought by the end of the first year, in the majority of cases, is some 150 nouns and 25 to 35 verbs. These he can recognize by speech-reading, can speak them orally and can write them.

For children who make poor and what is judged inadequate progress orally, some schools provide manual instruction. The manual means of conversation includes the use of the one hand manual alphabet by which words are spelled out letter by letter, A, B, C, D, etc.; it also includes the use of conventionalized signs. Common words may be either spelled or signed, for example, light is spelled (demonstrated) or it is signed (demonstrated), the placement and motion of the fingers, indicating the rays of light. For classroom purposes finger spelling is given decided preference over the use of the sign language.

While the above is a very brief presentation of the oral and manual means of instruction it is probably sufficient to serve as basis for discussing some of their social aspects.

Oralism seeks to make the deaf child a participating member of the hearing world. In this connection one frequently hears the phrase "Make the child normal." The fact that the practical accomplishments of oralism fall considerably short of this ideal does not materially lessen the appeal of such phrases to the majority of parents and the general public. This appeal combined with the desire of parents to have their children live at home and attend a special school, accounts for the large number of day schools for deaf children, all of which are purely oral schools. Oralism occupies a definite and useful place in the socializing of deaf children. The child who becomes adept in speech-reading and achieves clear speech enjoys an advantage over the child who is not so fortunate in these accomplishments. It is a fact, however, that most hearing people would find only a very small percentage of deaf children with understandable speech and good speech-reading. The large majority find conversation with anyone but close acquaintances difficult and will ordinarily resort to pad and pencil. In considering the social aspects of oralism this must be taken into account for it means that the general public will find that conversation with the ordinary deaf person must be carried on by means of pad and pencil. Furthermore, even the few who do have good speech are often reluctant to make use of it in talking to strangers. Some fear that they will mis-

pronounce words. They know of course that hearing people frequently mispronounce words, but fear that their mispronunciations will not be of the ordinary variety. Thus a deaf man may make three syllables of the word Chinese and call it Chin -e-see; there is nothing in the word itself to guide him. Right here, let me say that it does not take much of a defect in speech to distract ordinary listeners; when this happens their attention focuses on the defect rather than on what is being said with the result that the sentence has to be repeated. If the deaf person is sensitive about his speech, he becomes more reluctant to use it in public after a few such experiences. An acquaintance of mine is a capable and intelligent deaf woman. She is an excellent speech reader. Her speech is easily understood and therefore when she was a student in Gallaudet College, the national college for the deaf in Washington, she was frequently called on to address hearing groups. On one such occasion when she was addressing a group of hearing teachers she happened to look down into the front row and see one woman say to another, "It's remarkable, but isn't her voice peculiar?" She said that it took her years to get over that remark.

Speech-reading is regarded by the ordinary individual as something akin to another sense. It is not surprising therefore that usually too much is expected. There are of course the few whose speech-reading ability is amazing and such cases have been dramatized and publicized. Because a man is a good speech-reader, people expect him to be able to sit in a dimly lit church, at a considerable distance from the minister and understand what is said. Several profoundly deaf people have attended Ohio State University. Usually they get very little from the lectures through speech-reading. The instructor paces back and forth, or draws a diagram on the board, explaining it as he draws. Scattered student discussions in large classes are equally impossible to follow. As might be expected under such difficult circumstances, the percentage of deaf people who are able to attend colleges for the hearing is small. Those who do generally have some one take notes for them. Through conferences, assigned readings and reports they are able to cover the courses. The majority of the deaf who attend college go to Gallaudet College, a federally supported institution in Washington, D. C.

Some speech formations are relatively easy to read; others are quite difficult. Because a speech-reader has understood a greeting such as "How are you?" most hearing people assume that he will understand whatever follows it, even if it happens to be a sentence like "It's a nice day, isn't it?" The latter expression will try the best of speech-readers as many of the speech formations involved are not discernible to the eye.

There are numerous other stumbling blocks for the speech reader. About half of the words used in ordinary conversation have other words of similar appearance but different meaning. As an example the following words present practically the same appearance: main, made, mate, bait, bayed, paid, pain, pained, paint, pate. He depends on the context to determine which word has been used. If you were to use the cliche "sweet sixteen," it would be read as such because of the context rather than "sweet sixty," which presents the same appearance.

Another pitfall for the speech-reader is the effect of modulation, which he misses entirely. By modulating the voice we can change the whole thought of a sentence.

It must be remembered that speech movements are fast, some of them are concealed and the differences between many of them are fine. Furthermore, no two people speak alike. Placed in a group of hearing people, the speech-reader finds himself at a decided loss, because of the rapid shifts in conversation and the fact that he must pay close attention to get what any one of them is saying.

In spite of these difficulties speech-reading is of inestimable value and the social advantages apparent. In our schools for the deaf these social and educational advantages are given full consideration. Speech and speech-reading can be of real value to an individual even though he may not be able to converse with every stranger through these media. If oral conversation is sufficiently intelligible for home and school use it is of practical value. Through it a child becomes a participating member in the life of a hearing family. The probability is greater, at least in most cases, that his parents will talk to him in complete and connected sentences. Otherwise the tendency is to write or laboriously spell out with the manual alphabet clipped phrases or single words. Generally speaking, hearing parents do not acquire a facile use of the manual alphabet or the sign language. This matter of unrestricted conversation in the home is an important factor in the child's acquisition of language, which is a major problem with deaf children.

Educationally there is a sharp difference of opinion as to the extent to which oral training should be pursued. Some schools hold that all deaf children should be orally taught and offer nothing but oral work in their schools. Generally these schools contend that a child will progress as satisfactorily by oral means as by any other; if they make poor progress in an oral class, their progress will in any case be poor and the end values of oral training will be of greater value.

Other schools hold that while oral instruction is both desirable and advisable in the majority of cases, that there is, never-the-less, a sizable number of children for whom it is not a practical approach to either their educational or social problems. The majority of the residential schools for the deaf in the United States are in this group. These schools offer both oral and manual types of instruction, that is they have classes that are orally instructed and classes that are manually instructed. They contend that when it is clearly demonstrated that a child's speech-reading ability is so inadequate that he can get only random words and his speech is unintelligible, even to those who know him well, then it is time to substitute some other means of communication. Of the two considerations, more weight is given to his speech-reading ability. In such cases these children are transferred to classes that are manually instructed. For instructional purposes the manual alphabet is given preference over the sign language because it involves extensively the use of language. While the sign language can be used to convey ideas it does little for the individual in terms of a reading or writing vocabulary. A person may know a number of signs without being able to manually spell or read the written equivalent of a single

one of them. A few years ago an illiterate deaf woman called at our school. While she could neither read nor write she could carry on an intelligent conversation through the medium of the sign language. For the child who sits bewildered in an oral class, the manual class, through the use of the one-hand alphabet, provides an easily understood means of communication. These schools hold that they will educate children orally if possible; if it is found impractical to do so, further insistence will defeat both educational and social purposes.

The oralistic view-point is that through speech and speech-reading the social field of the deaf person is so widened as to bring him into normal or at least more acceptable relationship with the hearing world; the manualistic viewpoint grants that this is true in some cases but contends that since free social relationship with the hearing world is denied to the majority of deaf people, because of the inadequacy of their speech and speech-reading, they are automatically isolated from the hearing. Therefore, they believe that the social field, in such cases may best be enlarged through the medium of the manual alphabet and the sign language, for it brings normal relationships within the group, whereas none would be possible otherwise.

Manual conversation is a mixture of signs and finger-spelling. Signs are used for the common words; finger-spelling for proper names, technical or unusual words, and sometimes short words. The speed of manual conversation is only slightly less than that of normal speech. For a sizable group of the deaf it is a living and fluid means of communication; it gives spontaneity to their social events and is a necessary part of their lives. As it is clearly distinguishable at a distance, it is used for lectures, sermons, and plays. It is commonly used at social gatherings of the deaf. At any such gathering may be found a number who have had oral training but for social purposes, find fuller participation and greater social satisfaction in group activities through the medium of signs and finger-spelling.

With respect to both the oral and manual methods of communication it must be remembered that each has its function and each contributes to the happiness of a large group.

The acquisition of language is a major problem for the deaf. From childhood through adult life they struggle with the idioms and irregularities of the English language. A little girl who had gone home for the summer wrote of the good time she was having. In her letter she said: "I am hot water in the face," which was her way of saying that it was warm and her face was covered with perspiration. Not hearing words and phrases used countless times, it is not surprising that the deaf are at a disadvantage. The fine distinctions made in language are difficult for them, hence they may express themselves rather bluntly. The peculiarities in the written language of a deaf man attract more attention than the grammatical mistakes of a hearing man. Because of these peculiarities in English, hearing people sometimes underestimate the deaf individual. However, language difficulty is undoubtedly one of the most burdensome concomitants of deafness and its effect is more profound than is generally realized.

One of the commonest misconceptions about deaf children is that

they are a morose and unhappy group. This concept is fundamentally untrue. The little deaf child is isolated and feels it when in the company of little hearing children. He is naturally bored and unsocial in such circumstances. Brought to school and associated with other deaf children he is soon a happy and participating member of the group. These children meet on an equal footing and in the give and take relationships, self-reliance is developed. School life with its more normal associations brings about a change from a self-centered little child to a more social individual. Under such conditions many of the pre-school behavior problems disappear. It is frequently observed by teachers who have taught both deaf and hearing children that as a group the deaf children are better behaved. Recently a hearing survey (5) was made in the Boys' Industrial School. In over 700 cases we found not one profoundly deaf boy and only the normal incidence of hearing defects. From this it appears that hearing disturbances do not precipitate gross behavior problems.

Schools for the deaf, like schools for the hearing, have children who in mentality range from superior to dull. While Pintner (6) places the I. Q. of the deaf as being close to 80, on the average, the fact remains that it is much more difficult to establish I. Q.'s in the case of the deaf than in the case of the hearing. From the standpoint of adjustment and ability, it is significant that the adult deaf population is largely self-supporting. With the exception of those who teach in schools for the deaf, very few enter any of the professions. Occupationally, large numbers of them are to be found in the skilled and semi-skilled trades with good industrial and employment records.

In this day of governmental benefits for various classes, it is noteworthy that the deaf neither seek nor want pensions for their group as such. In this state they maintain and manage their own home for the aged and infirm deaf. They resent any gesture of charity. Beggars professing deafness are almost always impostors. The deaf make good citizens and contribute to the general welfare. They neither feel, nor want others to regard them as an unfortunate group.

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THE DEVELOPMENT OF HIGH VOLTAGE FOR THE PRODUCTION OF NEUTRONS AND ARTIFICIAL RADIOACTIVITY

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Eight years ago neutrons and the phenomenon of artificial radioactivity were discovered, following closely on the first work on artificial transmutation of the elements. In the years that have followed there has been a tremendous advance in our knowledge of fundamental physics of the atom as a result of these discoveries, a big development of equipment for producing and measuring the new radiations, and a wide recognition of their great potentialities for medicine. I understand it to be the function of our symposium this morning to make a rapid survey of this field from the particular standpoint of the cancer problem. In opening the discussion, I shall undertake only to present the physical side of the subject, properly leaving to my associates a discussion of the biological and medical phases.

Let us start by recalling that we now know that the atoms of matter are made of a central nucleus, composed of protons and neutrons and hence charged electrically positive, surrounded by enough electrons to make the atom as a whole electrically neutral. All the development of atomic physics from 1912 to 1930 was concerned with the study of the outer electronic structure—the decade from 1930 to 1940 has seen the interest shift almost entirely to the internal structure of the nucleus.

In solid bodies the atoms are packed in about one hundred million to the inch and the nucleus itself is about ten thousand times smaller in diameter. The atomic nucleus is the smallest thing whose structure is studied by man. The principal means of study has been by observation of what happens when atomic nuclei are struck by ions of hydrogen or helium which have been artificially accelerated to high speeds by means of high voltages. The bombarding ions need the high speed because they are charged positively and so are repelled by the nuclei, hence unless they have very high speeds they do not get close enough to produce any effect.

In the latter 1920's when physicists began to turn their attention to the nucleus, it was thought that several million volts at least would be needed to give the particles enough energy to effect nuclear transmutation. And at that time there was no known way that appeared practicable for getting more than one million volts. Cascaded transformers had been used up to one million volts or so. Electronic rectifiers in combination with transformers had been developed up to several hundred kilovolts. But then two developments occurred which opened up the subject. In the first place, theoretical applications of wave mechanics showed that the voltages needed were not nearly so high as at first thought. This theoretical prediction led to discovery that light

elements could be transmuted with relatively low voltages—several hundred thousand—although at such voltages the yield is very low and rises exponentially with the voltage.

The other important development was the introduction of two means of getting particles of extremely high energy. These are the cyclotron of Professor E. O. Lawrence of Berkeley and the belt-type electrostatic generator of Professor R. J. Van de Graaff of the Massachusetts Institute of Technology. These made possible the production of high energy beams of positive ions for production of neutrons, artificial radio-active materials, and nuclear research in general. The principle of operation of each of these is well-known to this audience. In the cyclotron there are no extremely high voltages on different parts of the apparatus. Instead the ions are caused by a magnetic field to move in a spiral path while gaining energy from an alternating electric field. In the belt generator the high voltage is obtained by carrying charge to an electrode with an endless cloth belt. The maximum attained voltage depends on the breakdown strength of the dielectric around this high voltage design. This requirement leads at once to very large sizes and special means of insulation. Both types of equipment, when built on a scale sufficient to provide several millions of volts, are quite expensive—somewhere in the neighborhood of $100,000 being the amount needed.

The cyclotron started in 1930 with a very small model built by Lawrence, then a working instrument built by Lawrence and Livingston which gave 1 million electron volts (Mev.) protons. This was followed by another with a magnet having pole-pieces 37 inches in diameter which attained about 6 Mev. and last year by completion of another having 60 inch pole pieces which gives 16 Mev. deuterons and 32 Mev. alpha particles. Now Lawrence is busy with the details of a huge project involving a cyclotron with pole pieces 184 inches in diameter, the magnet of which will weigh close to 5000 tons, which will produce deuterons of some 150 Mev. energy. The project is estimated to cost in the neighborhood of $1,500,000 of which some two-thirds has been provided by the Rockefeller Foundation. In the same period there has been a very widespread recognition of the importance of this research tool as evidenced by the fact that there are some thirty cyclotrons in the world, either built or building, mostly in the United States, and mostly financed in the expectation that they will prove valuable research tools in medicine.

Going along with this story of steadily increasing voltage, the "cyclotroneers" have made an enviable record in improving the total beam current, the latest being a total of 300 microamperes of deuterons at 16 Mev. on the 60-inch cyclotron. This means practically 5 kilowatts of power in a form available for intense nuclear disintegrations. Just a few years ago we heard of currents of 0.1 microampere. Now currents well above 10 are commonplace and many cyclotrons are getting close to 100 microamperes of beam current.

The first large belt generator is the one built by Van de Graaff at Round Hill, Massachusetts. This attained very great voltages, around ten million, but the great difficulties associated with building a large vacuum tube in which to accelerate the ions with this generator were

never successfully overcome. The tube was designed for horizontal operation, which introduced great difficulties of support. The first successful application of the belt generator principle to the study of nuclear physics is due to Tuve and Hafstad of the Carnegie Institution of Washington. Their generator with a two-meter sphere worked successfully to about 1200 kilovolts, and they usually have had available about 1 microampere of analyzed beam current. Later the Round Hill outfit was moved to the campus of the Massachusetts Institute of Technology and sat up in a different way to permit the installation of a vertical discharge tube. In this form it gets about 2500 kilovolts. This laboratory has principally applied the outfit to studies on the ultra hard X-rays produced when electrons of this voltage strike a metal target. Most X-ray physics and all radiological experience hitherto has stopped at 1000 kv., so we may hope for many interesting results from Cambridge.

About five years ago, Herb at Madison, Wisconsin, made the first really successful application of the use of compressed air as an insulating medium to improve the attainable voltage with a belt generator. Working with a pressure tank about 6 feet in diameter and 14 feet long, he built a machine which gives 2.5 million volts. The great gain in compactness which compressed air insulation gives is apparent when we realize that Herb's outfit in a small basement laboratory room gives essentially the same voltage as the large M.I.T. outfit which requires a good-sized building to house it.

With this experience to go on, the decision was made to build a large pressure insulated belt generator at the Westinghouse laboratories. This has been in operation about a year, as has also another similar one at the Carnegie Institution in Washington. Our machine is operated successfully at 4000 kilovolts with proton beam currents of about 1 microampere. The Washington machine has shown a similar performance. Two more pressure insulated belt generator outfits of intermediate size are now nearing completion, at the University of Minnesota and at the University of Pennsylvania.

I am sure that people who are closely interested in this subject would like me to say something about the relative merits of the two means of obtaining high energy particles. This is a quite complicated subject—and there seems to be no one who has had close working experience with both types. The Washington group soon will be in this position, for they are now building a large cyclotron like Lawrence's present large one to supplement the work of their large belt generator.

Since yields of neutrons or of radio-active materials go up roughly exponentially with voltage and directly with current, there is no question but that a cyclotron is at present superior to the belt generator as a strong producer of radio-active materials or of neutrons. And it does not seem likely that the belt type generator will catch up in total voltage and current for some time to come, so as a production instrument the cyclotron seems quite superior. In the belt generator the generator itself is capable of providing much greater currents—the crux of the problem is in the ion source at the high voltage end of the vacuum tube.

The main advantages of the belt generator seem to be as a scientific instrument and as a means of studying ultra-hard X-rays. The cyclotron

cannot accelerate electrons owing to their light mass and high relativistic variation of mass. Moreover, the different particles in a cyclotron beam do not appear to be nearly so homogeneous in energy as the particles in the beam in a steady belt generator. In our outfit at Westinghouse, we feel the variation is scarcely more than ± one-tenth per cent, whereas I think all cyclotron beams show a range of about ± 10 per cent, although it is hard to get definite information on this point. This makes the belt outfit an ideal instrument for precision measurements of resonance levels in nuclei and for onset thresholds of certain endoergic reactions.

It appears, therefore, that the two machines are more complementary than competitive, and that each is destined to play an important part in the continuing development of nuclear physics.

Ornithology Laboratory Notebook

The first part of this notebook (pp. 1–54) deals with laboratory studies of topography and anatomy, classification, nests, and distribution of birds. The remainder consists of sheets for the study of individual species (pp. 55–156), field check lists (pp. 157–204), and 180 outline drawings of birds for coloring. The pages for individual species studies contain a map of North and South America, and space for notations on some 20 points about the species.

The changes in this edition are intended to make it more useful in other parts of the country than New York State. The keys have been enlarged to include all orders and families of North American birds, and 18 new outline drawings have been added. Some of the outline drawings are somewhat generalized and can be used for any of several similar species. Blank spaces have been added to the field check lists.

The evident emphasis in an ornithology course which follows this notebook is taxonomy and classification. The sheets for individual species are very detailed, and filling them out will probably become a chore rather than a learning process for the student. The value of the notebook would be increased by a simplification of these species sheets, and by the inclusion of some suggestions on field study and identification, ecology, censusing, plumages and coloration, and a bibliography.

The data given on distribution, which give the student an idea of what birds to expect in the field, and the excellent illustrated key to nests, are perhaps the two outstanding features of this notebook.

The fact that this notebook is now in its fourth edition is evidence of its usefulness in a course in ornithology.—*D. J. Borror.*

Ornithology Laboratory Notebook, by Arthur A. Allen. v+204 pp. Ithaca, Comstock Publishing Co. Fourth Edition, 1941. $3.00 (paper bound).

A COMPARATIVE STUDY OF NEUTRON- AND X-RADIATION UPON BIOLOGICAL TISSUES IN THE CANCER PROBLEM

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The changes observed in irradiated biological tissues are believed today to be due basically to the ionization of tissue atoms. To the biologist and the radiation therapist, modern physics has presented many new ionizing sources in the form of artificially induced radioactivity in elements normally stable. All of these are of potential value in the field of cancer therapy.

At the present time interest is centered on the potential utility of fast neutrons in the treatment of cancer. More extensive investigations on normal and abnormal biological tissues have been carried out with fast neutrons than with any of the other products of research in the field of nuclear physics. Although the results of these studies are of interest to biologists in diverse fields, to those engaged in the treatment of cancer, there exists one primary question. Will neutron radiation be more effective than X-rays in the treatment of cancerous diseases of the human organism?

In studying the biological effects of neutrons, many investigations previously performed with X-rays have been repeated with neutrons. The results of these studies reveal the essential qualitative similarity of tissue reactions to neutrons and x-rays. Several workers have shown that neutron irradiation increases the rate of mutation formation in fruit-flies (*Drosophila melanogaster*) (1, 2); geneticists have employed x-rays for this purpose for many years. Certain phases of the process of mitosis (which determines cell division and therefore tissue growth) can be suppressed both by neutron and x-ray irradiation (3, 4).

The embryological development of Drosophila eggs is disturbed in the same fashion by x-rays and neutrons. The larvae surviving both types of irradiation demonstrate aberrations of organ development(5). Both radiations suppress the growth of wheat seedlings and inhibit cell division of the fern spore.

Experiments carried out on mammalian tissues demonstrate that identical changes are produced by both radiations. Whole body irradiation of mice with neutrons and x-rays produces death of the animals; the blood-forming tissues, the lymphoid tissues and organs, as well as the lining cells of the intestines are damaged or destroyed (6). The characteristic changes seen in the blood cell picture of animals irradiated with x-rays is found with neutron irradiation. Experiments with transplantable mouse cancers have shown that suppression of the growth of the tumor transplants is brought about by both radiations (7).

More recently with the development of collimated neutron beams, the reaction of skin to neutrons has been observed in rabbits and in man. The changes appear to duplicate those following x-ray irradiation.

Thus the effects of neutrons have been observed in a variety of biological processes: mutation production, suppression of mitosis, inhibition and impairment of embryological development, suppression of cell division and of growth of tissues; the destructive action of this radiation on mammalian tissues has been demonstrated. In each instance it seems that, in kind, the changes are of the type seen following x-ray irradiation.

Certain quantitative aspects of neutron ionization merit consideration. Early in their work Lawrence and his associates found it convenient to measure neutron ionization with the same small ionization chamber as is used currently to measure x-ray ionization (8). The work of Gray on the measurement of gamma ray energy indicates that under certain conditions the use of such chambers for measurement of neutron ionization is valid (9). When used with x-rays, the scale units represent roentgens, the international unit of ionization quantity; when used with neutrons, the same unit deflection has been arbitrarily termed the n-unit.

The relationship of the quantities of ionization in tissue that the two units represent has not been definitely determined as yet; this is a matter of considerable importance. By irradiating fern spores with alpha particles Zirkle demonstrated that the biological effectiveness of the radiation was greatly influenced by the ion concentration along the path of the ionizing particle; the biological effectiveness varied approximately as the 5/2 power of the ion concentration (10). In view of the greater concentration of ions along the tracks of protons and other recoil particles produced by neutron irradiation, a greater biological effectiveness was to be expected for neutrons than for x-rays.

A number of comparisons on various biological test objects have been carried out by Lawrence and his associates (7, 11) and also at the University of Michigan (12); it was found that in apparently every instance neutrons were more effective than x-rays in producing equivalent biological reactions. The differences in efficiency ranged from a factor of 2 in inhibiting hatching of Drosophila eggs to a factor of almost 12 in suppressing organ growth in wheat seedlings.

Although these figures cannot be accepted at face value until the relationship between the two units of ionization has been clearly established, there is indirect evidence to indicate that the greatest possible error probably does not exceed forty per cent (12).

In an interesting report, Zimmer and Timofeeff-Ressovsky have shown that neutrons are less effective than x-rays in affecting the mutation rate of Drosophila (1), and have demonstrated that, since mutation production depends on the formation of one ion pair in a gene, a decrease in effectiveness should be obtained with the type of distribution of ions created by neutron irradiation. For those biological reactions which require the formation of multiple ion pairs in the so-called "sensitive" volume, the distribution of neutron ionization should be more effective than that obtained with x-rays.

It appears then that in neutrons we possess not only a radiation which produces changes similar to those seen with x-ray irradiation but a radiation which is apparently of greater effectiveness in exciting reactions of the kind we are concerned with in the treatment of cancer.

This radiation probably will be more lethal than x-ray in its action on the cancer cell but does this mean that it will be more effective in treating cancer in the human body?

In order to be effectively employed, a radiation must act in a selective fashion: the tumor must be destroyed but the regional normal structures must be preserved. It is because of the existence of such a favorable differential action on cancerous and normal tissues that x-rays and gamma rays have attained a measure of success in the treatment of malignant neoplastic diseases. Other factors being equal, neutron radiation will be more effective in the attack on cancer in the human organism if its differential action is found to be more favorable than that of x-rays. The absolute biological effectiveness is only of secondary importance.

Because collimated neutron beams were not available until recently, it was necessary to approach the problem of the differential or relative actions of x-rays and neutrons in an indirect manner. From a broad biological viewpoint a cancer and its regional normal tissues represent related tissues in the same organism and the basic problem devolves to a consideration of the comparative action of neutrons and x-rays upon two such tissues.

In the first investigations by Lawrence and his associates, a number of different types of biological test objects were used: Drosophila eggs, fern spores, transplantable mouse tumors, mice, and wheat seedlings (7, 11). It was found that the relative effects of the two radiations upon these organisms presented decisive differences. Had these experiments indicated that the relative effects of the two radiations upon such diverse types of biological tissues were consistently the same, certainly it would have appeared highly improbable that a remarkable difference could be expected for two tissues as closely related as cancerous and normal cells in the human organism.

In order to create a situation in which the relative effects of the two radiations could be studied on tissues as closely related as a tumor and its regional normal structures, Drosophila eggs were irradiated at different stages in their development (12). Here again though dealing with two sets of tissue in the same species of organism, significant differences were found. By irradiating wheat seedlings, the relative action of the radiations upon different organs (root and shoot) in the same individual organism was investigated and despite the essential similarity of the tissues composing these organs, the relative effects of the two radiations were found to be consistently different.

On the basis of the demonstration that differences in the relative action of neutrons and x-rays exist not only for distantly related but also for closely related biological tissues, it appears highly probable that a difference in the relative action of the two radiations upon cancerous and normal tissues may exist. The selective action of neutrons probably will differ from that of x-rays. As yet no evidence exists to indicate whether the selective effect will be more favorable or less favorable than that of x-rays; it is evident that this represents an incomplete solution of the problem. At the present time, at the University of California and to a lesser extent at Michigan, several collimated neutron beams

are being used in a direct attack upon the problem; a more adequate estimate of the potential usefulness of neutrons in cancer treatment may become available in the near future.

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Magnetism and Very Low Temperatures

Magnetism and Very Low Temperatures, by H. B. G. Cassimir is a tract based on a series of lectures delivered by the author at Cambridge in the spring of 1938. The treatment is contained in seven chapters of which the first is introductory in character. The second chapter is devoted to classical theories and experimental methods. In chapter three the author presents a brief and concise treatment of the essentials of the quantum theory of paramagnatism. Chapter four is devoted to the experiments on adiabatic demagnetization and in chapter five the author gives a theoretical discussion of paramagnetism at low temperatures. Chapter six is given over to experimental results and finally in chapter seven is discussed the relaxation phenomena.

Like many others of the tracts in this series of publications the material is presented in a very comprehensible manner. It is presented on a level which can be digested by graduate students with an intermediate training and gives the reader a good insight into the problem of magnetism and very low temperatures.

—*H. H. Nielsen.*

Magnetism and Very Low Temperatures. H. B. G. Cassimir. Pp. 93+ix, Fig. 14. Cambridge, At the University Press, 1940.

CANCER: CLINICAL AND EXPERIMENTAL ASPECTS

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Since civilized man recorded his opinions on stone, papyrus or in the memories of man, cancer has been mentioned. The early Greeks, Hindus and Egyptions left recognizable descriptions of what they saw. It is probable when the Stone Age man noted his wife dying of something which he could not understand that it was a cancer. Crude surgery developed during the Middle Ages, but presumably no one was ever cured. The invention of the microscope was the next necessary step and then came the discovery of the cellular nature of the tissue structures about one hundred years ago. In the forties and fifties of the last century the classification of human tumors became the main subject of interest. Various hypotheses as to the causation of cancer were produced, the most important being that of Virchow, who believed that the appearance of cancer was usually correlated with chronic irritative processes, and clinical observers began to collect material to support this notion. The betel-nut cancer of the mouth in the East, and the Kangri cancer due to the native custom of carrying a basket of burning charcoal under the clothes for comfort in winter, which frequently burned the abdominal wall, are two examples. Many of these burns were followed by cancer. The Far East also offered the first examples of the parasites in the internal organs which ultimately cause human cancer. About 1875 Cohnheim introduced the idea that many of the more complex growths were the result of remnants of tissue left during embryonic development.

Attempts to transplant tumors occurring in domesticated animals were carried on for many years but failed completely until Loeb and Jensen at about the same time, that is in 1901 to 1903, found that spontaneous tumors in mice and rats were transplantable into the same species only. Shortly after this the Imperial Cancer Research Fund was established in England, with Bashford at its head. He was an aggressive, broadly trained pathologist and gave great impetus to cancer research. Another worker was the famous Paul Ehrlich, the inventor of salvarsan, who after a few years abandoned all attempts at cancer research but made important contributions concerning inoculated tumors during this period. The earliest studies were exploratory in direction and included the transplantation of tumors in animals purchased, in general, in the open market, and the observation of a host of phenomena following grafting, among them the prompt disappearance of a tumor, leaving the animal immune.

This false lead has wasted hundreds of thousands of dollars and literally thousands of years of labor. For thirty years investigators had been struggling to imitate the process of the spontaneous disappearance of tumors. Finally, Little, a geneticist, Tyzzer, a pathologist, and the

workers in the Institute of Cancer Research of Columbia University, began to insist upon the importance of pure strains as a culture medium for the tumors. Immediately all spontaneous cures ceased, no immunity could be produced by the inoculation of tumors, and a host of observations, biologically important but not pointing the way to any fruitful results, have disappeared into the scrap-basket of the forgotten.

It is now generally understood that the cancer cell is an individual in the body of the host and that some tumors may spring from a single cell. More rarely multicentric growths appear. It probably takes an individual cell a long time before it and its descendants make a sufficient mass to produce a noticeable tumor, years in fact in man and more rapidly in the shortlived rodents. The change in the cell is probably a mutation of some type or if the geneticists want to argue about the question of a "somatic mutation," let us leave the phrase to them and call it a change of some sort in the protoplasm and the nucleus of the cell. Once this change has taken place the new race lives as a parasite on the body of the host. There is ample evidence now that this is a permanent and irreversible change. A cancer cell cannot be made to revert to a normal cell, as was believed even a few years ago.

All the morphological and biological qualities of these inoculated tumors remain permanent over thousands of transfers. The Jensen rat sarcoma still looks as it did in 1903. Nevertheless, this new race has the same cell chemistry of the host in which it originated and, therefore, it does not incite reactions of the type induced by bacteria and foreign proteins. Hence, the search for immune reactions has been a continuous failure.

It was hoped that cancer could be diagnosed by serum or chemical reactions, but all efforts have so far failed, with the exception of the Aschheim-Zondek test. This is limited to one type of tumor and is based upon the stimulation of the ovary of the mouse or rabbit to form a hemorrhagic follicle owing to the production of hormones by the tumor. The source of these hormones are the chorionic cells from the placental structures which form in the teratomas of the testicle. The use of the Aschheim-Zondek test is not so much to make a diagnosis of the teratoma as to call attention to recurrences if such take place, as in that event the patient can be treated by x-ray. The seminomas of the testicle, the most frequent type of tumor, do not show any reaction to the Aschheim-Zondek test, as their cells are derived from the testicular tubules. In women with chorio-epithelioma of the uterus, a positive reaction is important if pregnancy can be excluded and if the reaction does not become negative, it shows that extensions of the growth have taken place in other parts of the body where they may be unrecognizable even by x-ray examination.

It was hoped also that in some way we might extract anti-bodies from animals with cured cancer which, when injected into a cancerous animal or a cancerous human being, would result in the destruction of the tumor. All this failed. A large series of experiments was carried on by Hodenpyl, who used the ascites fluid from a case of quiescent human cancer to inject numerous patients, with results which were startling at the time, but unfortunately no cures resulted. The injection of

damaged cancer cells, killed by heat, cold, radiation and chemical agents, was tried in the hope of inducing an immunity similar to that obtained by injecting dead bacteria, but without the slightest result.

It has been known for nearly 200 years that gas tar causes cancer in human beings. For a long period attempts were made to produce cancer in animals by this agent but, curiously enough, the experimenters used either dogs or white rats and the skin of these animals is not susceptible to this agent. If they had used white mice they would have succeeded in the first attempt, because the skin of the mouse is exceedingly sensitive to tar irritation. Yamagiwa, in 1915, showed that cancer could be produced in the ears of rabbits by tar painting. Many of these were only papillomas, but a moderate number of carcinomata can always be produced with an effective tar. The English, who are always interested in tar and the industrial oils because of the large number of cases of carcinoma which occur in their factories, continued these investigations and the most promising were those of Leitch and Kennaway. Kennaway showed, in 1925, that acetylene when heated yielded a cancer-producing tar, hence the substance which causes cancer in tar workers would probably be of that composition, that is carbon and hydrogen.

The spectroscopic study of many of the carcinogenic substances showed a characteristic fluorescent spectrum in the near-ultraviolet, and Hieger showed that 1 : 2 dibenzanthracene gave this same spectrum. Clar in Germany was the first to synthesize 1 : 2 : 5 : 6 dibenzanthracene and Cook, who was working with Kennaway, resynthesized this material and found it to be carcinogenic. A somewhat more powerful carcinogenic substance was obtained from gasworks tar and is known as 3 : 4 benzpyrene. In 1933, another carcinogenic substance, methylcholanthrene, was synthesized by Wieland and Dane. Cook investigated this compound and found it highly carcinogenic. Methylcholanthrene is derived from the cholic acids and this suggests the possibility that such a synthesis may take place in the body. Further studies have shown that beta-naphthylamine given by mouth or subcutaneously will cause tumors of the bladder and Japanese workers have produced tumors of the liver with orthoaminoazotoluene and paradimethylaminoazobenzene. Azotoluene causes cancer of the bladder and it is probable that 3 : 4 : 5 : 6 dibenzcarbazole produces not only cancer of the skin at the site of application but also tumors of the liver.

The method of action of these compounds is unknown and tumors have been produced in a variety of animals: mice, rats, rabbits and guinea pigs. Tests are going on with the longer-lived creatures, but the ape, for instance, which presumably has a life of some twenty or thirty years, would require three or four years' treatment to produce a tumor. For out of all these studies has arisen the fact that the time of appearance of a tumor with the same carcinogenic agent is correlated with the length of life of the animal. If a mouse lives two years, one-twelfth of that would be two months; if a human being lives 72 years, one-twelfth would be six years. It would be expected that if a mouse had a tumor in two months, which is the case, the human being might require six years, and such is also the case in connection with tar workers, x-ray injuries and a number of other cancers the origin of which we can determine.

Another experimental study has been the investigation of the effect of trauma on animal tumors in order to determine the possibility of a single injury causing cancer in human beings, a matter which is frequently discussed in the law courts. All the animal experiments showed that trauma had no effect on a tumor.

The three most important practical investigations which have come out of the laboratory are: (1) The demonstration by Tyzzer and Knox, that the massage distribution of animal tumors with small cells can be easily accomplished, while the fibrous types, such as the fibrosarcomata and some of the sarcomata with large cells could not be dislodged by massage, and the small-cell sarcomata metastasized extensively without massage. (2) It was shown that the incision of a tumor for removal of a specimen for microscopic examination was not injurious in animals when properly carried out. (3) Quantitative experiments using radium and x-rays on tumor particles and tumors in animals showed, twenty or more years ago, that animal tumors required large doses to destroy their cells, an important bit of knowledge which is just beginning to penetrate into human practice and reveals the lag between the laboratory and the clinic.

It is obvious that the laboratory research side has been in general more the laying of foundations and the removal of misconceptions, most of which were derived from bacteriological analogies. The investigation of cancer has really gained nothing from bacteriology. General biology, on the other hand, has greatly benefited by the discoveries of Rous, Gye, Shope and other workers who have studied the cancer problem from the point of view of the viruses. This does not mean that human tumors are with any probability connected with virus infections, but the fact that certain chicken sarcomas are is an important biological point and the recent demonstration by Rous that the Shope rabbit papilloma virus can act as an agent for the production of malignant growths in the rabbit by means of tar or the carcinogenic hydrocarbons was certainly a discovery of prime importance as regards general biology.

The real advances, however, which have been made in the last forty years on the cancer problem have not been made by the laboratory investigators. They have rather been due to mass attack on the problem and two vital discoveries in physics, that of the x-rays by Roentgen and of radium by Marie Curie. They have added immensely not only to diagnosis but to the treatment of cancer as well. It is scarcely necessary to mention before this audience what enormous facilities have been placed in our diagnostic armamentarium by the development of the x-ray technic. No one procedure in diagnosis has been so valueble in every phase of medicine and surgery as this.

Other improvements have taken place, all of them practically within the last forty years. Firstly, the development of asepsis, which was really concluded with the adoption of the rubber glove, in about 1895. Then there is anesthesia, which, of course, is always necessary for the prolonged surgery of cancer. Not only general anesthesia with ether, but also a host of modern anesthetics, both general and local, greatly facilitated the handling of the disease in surgery. Forty years ago the treatment of cancer was in the rudimentary stage and very few patients

were ever permanently cured or relieved of the disease. Today with the introduction of improved instruments, such as the gastroscope, bronchoscope, cystoscope, peritoneoscope, etc., the various internal organs of the body can be inspected and tumors can be seen and fragments removed for microscopic examination. While it is not always possible to see every carcinoma of the stomach or every bronchial carcinoma, nevertheless most of the tumors of these regions, even of small size, can be demonstrated.

Since 1895, a matter of only forty-five years, the whole development of an effective attack on cancer has taken place. This is due largely to experimental work on animals and the efforts of leading surgeons in this country and Europe. What we have learned from experimental physiology and pathology has in many ways directly helped in the traetment of cancer and added to our ability to attack the disease in parts of the body where no one had thought of attempting to do so with successful results ten years ago, yet such operations are now being done quite frequently, as in the case of carcinoma of the lung. Obviously, many of the internal cancers are seen so late that despite modern diagnostic efficiency nothing can be done because metastases have occurred throughout the body. But with the improvement in and extension of education which, of course, must go hand in hand with diagnosis, patients are coming earlier for examination and many are having annual or semi-annual studies made in order to eliminate the possibility of an inaccessible growth.

A good deal of this effort owes its success to the publication of large series of cases operated upon or treated by radiation which have survived for a five or ten year period. The American College of Surgeons has contributed much to this by the collection of some 30,000 recorded cases of cancer well for five years or more. This was done very easily, the figures coming mostly from the large hospitals in this country, and such a demonstration cannot help but be impressive and of value in aiding education. No one will listen with pleasure to a recital of the number of deaths from cancer. On the other hand, now that the profession is in a position to say that as a result of the last forty-five years' work and scientific study a real step forward has been made, people will listen eagerly.

An example of the change which has come has just been published by Schinz from the Radiation Clinic in Zurich, giving a complete review of their material as observed from 1919 to 1935, with no selection whatever. In this period 2529 patients were treated. In January, 1937, 15 per cent of the total were alive and apparently well. There could be added to this 2 per cent more who died from intercurrent disease during the period without symptoms of cancer, but they and the untraced cases, amounting to another 2 per cent, were rejected. Also, favorable palliative results were obtained in 54 per cent of the total. The patients referred to this Clinic are most of them inoperable and, therefore, represent a more or less hopeless group and the fact that 15 per cent of these hopeless cases can be cured now by radiation, when twenty years ago the effective use of x-ray was just beginning and probably all these patients would have died, shows what can be accomplished.

Another field in which there has been great improvement is that of cancer of the cervix. The League of Nations figures are astounding. Studies of many thousands of cases have been made from all over the world and about one-fourth of such patients are cured for five years or more. The interesting point in this is that the conditions are not very favorable for early diagnosis and in those cases in which the diagnosis was made early, there was a 40 to 50 per cent of five-year cures. But more important still is the fact that there were 5 per cent of cures in the hopeless and advanced types which have never been cured by surgery.

On the other hand, from a purely surgical standpoint, cancer of the breast is now being cured in about 30 to 35 per cent of all patients coming to the hospital for treatment and the early types are being cured in 75 to 80 per cent. This means that the tumor has been diagnosed microscopically and the patient has been followed for the elapsed five years.

This is an astonishing thing to one who like myself has watched the whole period of development of cancer surgery and radiation. During the time of my internship, for instance, from 1894 to 1897, only the very smallest and earliest superficial tumors were cured and no attempt was made to cure a cancer of the stomach, for example, of which the Mayo Clinic now reports a 5 per cent salvage. Most of our patients came so late that the operations today would not be undertaken. Now when a patient is considered inoperable, he is treated palliatively with radiation or surgery, or both, to prolong life as much as possible in comfort.

Principles of Genetics

It is indeed unfortunate when an otherwise excellent book is marred by a few gross misstatements of fact. Such is the case of the recent book, "Principles of Genetics," by Grace White. In man the inheritance of the blood groups is known to be due to triple alleles. No trait in man is more clear cut or more definitely established, yet the author states that the inheritance of the blood groups is due to duplicate factors.

On page 265 we find the following statements: "The chances for any one autosome from a paternal grandparent reappearing in a grandson is estimated at $1 : 2^{23}$ or one chance in 8,388,608. The grandson has one chance in six, however, of receiving the paternal grandparents' X-chromosomes, and this makes the study of sex-linked inheritance far simpler than the study of autosomal characters." These statements are obviously incorrect. There is no chance whatsoever that a boy received his X-chromosomes from his paternal grandfather. Moreover, the chances that he did *not* receive *any* autosomes from his paternal grandfather are 2^{23}, quite different from the author's statement. Sex-linked factors may be detected more easily in males because the recessives manifest themselves when present.

The book as a whole is very readable, and is written in an interesting manner. Mutations are used in the broader sense, to include chromosomal aberrations as well as gene mutations. The illustrations are both excellent and numerous. Aside from the errors mentioned above, the book is an unusually good elementary treatise of genetics.—*D. C. Rife.*

Principles of Genetics, by E. Grace White. 352 pp. St. Louis, The C. V. Mosley Co., 1940. $2.50.

THE CLASSIFICATION OF NERVE FIBERS

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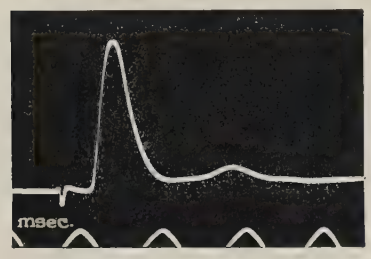
As more is learned about the mechanism of operation of the central nervous system, the characteristic of the mechanism that becomes the most impressive is the exquisite timing of the events. For example, if an impulse of subliminal effectiveness impinges upon a synapse, it leaves a trace which lasts only a few tenths of a millisecond. If within that time another impulse, likewise of subliminal effectiveness, arrives at the same region on the surface of the neuron, the two impulses together will raise excitation to the threshold, and a relayed message will be sent upon its way. Stated in other words, if the two impulses arrive at the synapse at an interval of separation longer than a few tenths of a millisecond, there is no transmission; and the local disturbance that each impulse produces dies out promptly, to leave the junctional area restored to its antecedent state ready for any new impulses that may be coming on. Transmission at any point thus depends upon the arrival of excitation from the various controlling centers in exactly the right time relations. Thereby the flow of impulses is always properly directed toward the end reaction appropriate to the conditioning data picked up by the body receptors.

The timing of impulses starts in the beginning of all reactions—in the sensory messages that report changes in the state of the body and in the character of the environment. At least no other interpretation explains as satisfactorily why sensory messages are carried at so wide a range of velocities. For some reason not at all well understood it is necessary for some impulses to shoot out ahead to prepare the central nervous system for other impulses that arrive later. In as simple an event as pricking the skin of the finger with a needle there is first a short burst of impulses carried in fibers conducting at 90 meters or more per second (20). Then there follow impulses at other velocities, many at about twenty meters per second; and finally there is a trail of impulses at about one meter per second. Before any of the last mentioned group arrives at the centers, a complex neurological event has taken place—the withdrawal of the hand; and the sensation of pricking has been appreciated. The sensation aroused by the slow fibers is still, however, that of pain indistinguishable qualitatively from the pain already felt. But in its setting it has a stinging, irritating character. It can be relieved by rubbing the spot, that is, it may be inhibited by sending into the central nervous system a flood of impulses carried in rapidly conducting fibers.

It is not my intention in the present paper to follow up this argument, but to let the observations stand as an introductory background to the main theme, which is the basis of the numerous velocities in nerve fibers. Visualization of the wide range of velocities can best be accom-

plished by showing what happens when a sensory nerve is artificially stimulated with an electrical shock of short duration. All the impulses start out together from the locus of the stimulus, but the fast impulses forge ahead. Thus, if a lead be taken at some distance from the point of stimulation, at the beginning of the action potential there are initially recorded the first impulses to arrive; and the other impulses are recorded later, at times inversely proportional to their velocities. As all the velocities are not equally represented among the fibers, the result is an action potential with distinctive elevations. The contour here presented (Fig. 1), taken from the saphenous nerve of the cat, is characteristic of all sensory nerves. It starts with a high elevation contributed by fibers conducting at velocities ranging approximately between 95 and 35 m.p.s. The high elevation is succeeded by a very small one in which velocities between 35 and 22 m.p.s. are represented; and this in turn is followed by a somewhat larger one representing velocities between 22 and 15 m.p.s. In the wake of the latter there are still a few impulses at a velocity slower than 15 m.p.s.



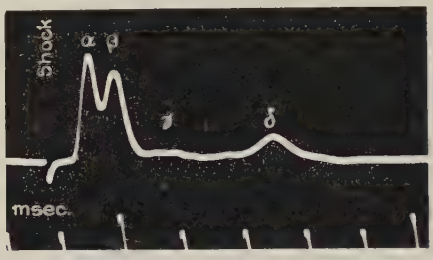


Figure 1 (left). Action potential of the saphenous nerve of the cat as recorded after 4 cm. of conduction from the stimulating cathode. The first disturbance in the line marks the moment of stimulation, and the interval between this point and the start of the first high elevation measures the conduction time of the fastest fibers. The potentials contributed by the other fibers follow in succession.

Figure 2 (right). Action potential of the saphenous nerve of the rabbit as recorded after 4 cm. of conduction.

The first elevation is actually a fusion of two elevations, as can be shown in leads at long conduction distances, or more easily in the nerves of young animals (Hursh), or in the saphenous nerve of the rabbit (Fig. 2). For the sake of ease of reference, the elevations have been given names. The terminology has undergone a series of revisions in the course of its historical evolution, and it is not entirely satisfactory. Subject, however, to the definition here given, it seems well to adhere to the original designations in terms of the Greek alphabet; and the elevations are accordingly called alpha, beta, gamma, and delta. Collectively the fibers so designated are spoken of, for reasons that will appear later, as the A group. The group takes in all the medullated fibers of somatic nerves. The remaining, unmedullated fibers are included in the group known as C. In order to visualize the potentials in C fibers it is necessary, because of their small size, to resort to much higher amplification

than is necessary for the A fibers; and because of their slow velocities, to much lower sweep speeds, (Fig. 3).

After this preparation we are ready to penetrate further into the velocity problem. At the outset it may be stated that the size of the fibers is to play a large part in the argument. The first association of velocity with fiber size was made by Göthlin in 1907, long before the advent of the modern vacuum tube era in electrophysiology, and at a time at which knowledge about velocities was in a highly fragmentary state. Göthlin's contribution is to be recalled merely because of its inherent fundamental idea, as his treatment was a theoretical one based upon the structure of axons and the Thomson cable equation, and his deductions are not in accord with the facts about conduction as they are now known. The association of nerve function and fiber size again

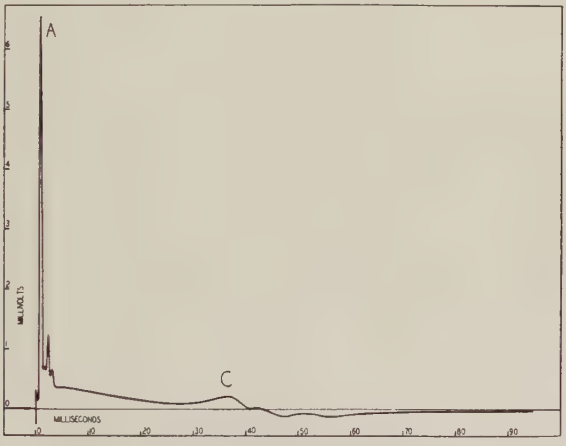


Figure 3. Drawing of the action potential of the saphenous nerve of the cat, constructed from two records made at different amplifications and sweep speeds. Activity of all the fibers is shown. The A complex depicts activity in the same group of fibers represented in Figure 1 (but from a different nerve). The interval between the A and C elevations is filled in by the negative after-potentials of the A fibers.

appeared independently four years later in the work of Lapicque and Legendre. What these investigators actually did was to measure chronaxies and correlate them with the axon size, and their statement that the velocity in the fibers was in direct relationship with the size was purely an inference. As it has turned out, it has been proven that the inference was correct, but that the chronaxie-size relationship had to be abandoned. Blair and Erlanger in 1933 demonstrated that the chronaxie of frog fibers is almost constant in the velocity range between 7 and 30 m.p.s.; and Lapicque, as the result of some experiments performed with Pézard, has now modified his view and gives prominence to his older idea that chronaxie is a parameter of the protoplasm of the fibers.

In 1924 it was my good fortune to be working in Prof. Lapicque's laboratory at the Sorbonne. At that time the observation that Erlanger and I had made of the temporal dispersion in the action potential of nerves was very recent, and when I showed the records to Prof. Lapicque he immediately said that the velocity variation at the root of the dispersion must be attributable to fiber-size variation. Thereupon we proceeded to test the hypothesis (14). Because of the supposition that chronaxie might be related to the cross-sectional area of the axons, which was incorrect although we did not know it, we tried first to correlate velocity and area, but with no success whatever. Then we tried the first power of the diameter and the result was much more promising. At this time the work was interrupted by my return to St. Louis, and it was there taken up again with Dr. Erlanger.

Before going further it will be necessary to say a word about the method employed. The first step was to record the action potential at a known distance of conduction. Then the nerve was sectioned and a distribution map of the fiber diameters prepared. The velocity of the fastest fiber, which could be read from the record, was assigned to the largest fiber and the velocities of the other fibers were calculated therefrom on the basis of the diameter ratios. There was experimental evidence to show that the spikes all had the same duration and it was calculated that the recorded heights of the spikes should be as their cross-sections. Accordingly, the further procedure was to calculate the potential that fibers of each size should contribute to the compound action potential, plot the result as spikes at the conduction times determined by the velocities, add the spikes together, and compare the sum with the action potential as actually recorded. The resemblance of the reconstructed and the recorded potentials was remarkably close, and it was felt that at least a first approximation to the size rule had been found.

But, whatever there was of satisfaction was only that which the ignorant can enjoy. And it was short-lived. The situation may be compared to the knowledge of geography before America was discovered. Our fiber world ended at gamma, with an uncertain and nebulous delta in sight beyond it. As soon as high gain amplifiers were built it was possible for us—that is, for Dr. Erlanger and myself—to see that there were two well-defined elevations that had not previously been recognized, those now labeled delta and C. With the finding of these elevations the fiber problem became wide open again. Reconstructions made under the rules gave so inadequate a fit with the recorded action potential as to indicate that something was wrong. Indeed, it was even doubtful whether the method was applicable at all, as it could be expected to work only within a homogeneous group of fibers. A new question was raised: How many kinds of fibers are involved? The natural inference was that there were three kinds. But there was difficulty in connection with the second elevation, which was then labeled B and is now labeled delta in mammalian nerves. The fibers in the B elevation in frog somatic nerves were obviously not homologous with those in the mammal. A solution of the difficulty came through a parallel study of visceral nerves made by Bishop and Heinbecker.

These investigators delimited the B elevation in visceral nerves and showed through estimations of the spike durations and the refractory periods that the constituent fibers are different from those in the C elevation and in the alpha portion of the A elevation. In the frog the B fibers pass through the grey rami into somatic nerves, but they do not do so in the mammal. The fibers which produce the elevation, then labeled B, in the action potential of mammalian somatic nerves were shown to have properties much closer to those of the fast A fibers than to those of the B fibers of visceral nerves. Thus, if they really were different from A fibers, a separate, fourth class had to be defined.

Without important additions or changes the formulation remained as here stated until 1933, when Blair and Erlanger introduced a radically new idea. On the basis of data obtained upon single frog-axons,

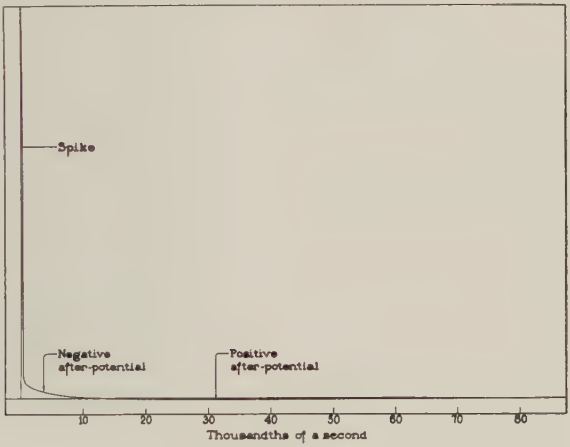


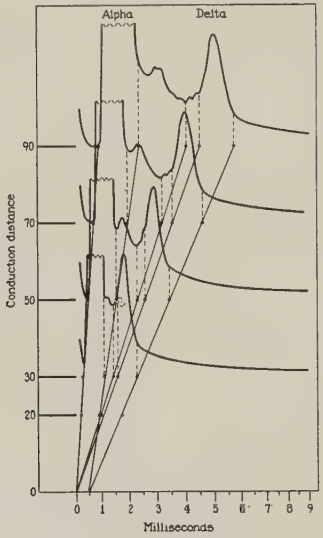
Figure 4. Course of the whole potential cycle in a unit mammalian A fiber, drawn to scale from two records made at different amplications and sweep speeds. It can be seen from the almost invisible size of the positive after-potential in this drawing that much higher amplification is needed to reveal the after-potentials than is needed for the recording of the spike.

which indicated that from the fastest fibers down to those conducting at one meter per second there is a progressive increase in the duration of the spikes and the refractory periods, these investigators proposed that the fibers make up a continuously varying series; and they felt that the division into groups was unjustifiable.

In the past few years our laboratory, for two reasons, has taken a renewed interest in nerve fibers. The first and foremost reason was that there was a need for more precisely determined constants of mammalian fibers as equipment for the interpretation of the events that take place in the central nervous system. The second reason was to prepare the way for a return to the old problem of velocities. With the new information there came new tests for homogeneity. Previously the classification of fibers had depended largely upon the properties of the spike. But the spike is only part of the action potential. The whole action potential is

made up of three parts: first the spike, then a negative after-potential, followed by a positive after-potential (Fig. 4). The after-potentials are even more typical of the fibers than the spikes.

Every precaution was taken to keep the nerves in the best possible physiological condition. Unlike the spikes, which are very stable, the after-potentials are extremely labile. Environmental changes alter both their form and duration; therefore, they are very sensitive indicators of the state of the nerve. With this lability it may perhaps be asked how one can know what the normal is like. The answer is the



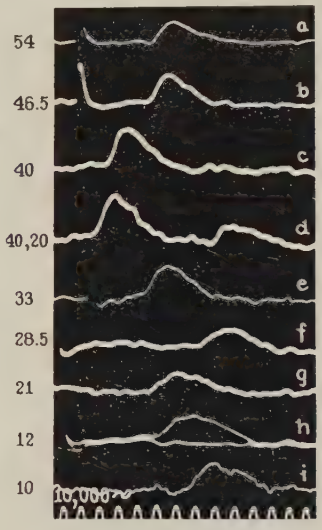


Figure 5 (left). Action potentials in the sphaenous nerve of the cat recorded at the distances indicated on the ordinates. Because of crowding in the figure, only the projection of the events on the base line is shown at 2 cm. of conduction. The time interval subtended by the converging lines at the axis of abscissas measures the duration of the alpha and delta spikes. (Gasser and Grundfest, 1939.)

Figure 6 (right). Unitary axon spikes arranged according to velocity (simultaneous responses in 2 fibers in record i). The velocities are marked at the left in meters per second. (A spike of a 90 m.p.s. fiber is shown in Figure 8.) All records have the same time scale. (Gasser and Grundfest, 1939.)

following. The after-potentials determine a cycle of excitability, and if the form of the after-potential corresponds exactly to the excitability as determined on the same nerve *in situ* under its natural perfusion of blood, there is every reason to believe that the fibers are normal.

Alpha spikes recorded from single axons in spinal roots last 0.4 to 0.43 msec. (Fig. 8). In nerve fibers they may appear at this duration or a few hundredths of a millisecond longer. But the last few hundredths of a millisecond cannot be considered as being significant, as the recorded duration depends in part upon the material from which the spike is led—that is, upon the distance beyond the active point at which the potential is picked up. Now let us inquire into the range of the spikes to which

this duration applies. Does it extend to the delta elevation, for example? The quickest way to become oriented as to the answer is to make an extrapolation of the duration of the elevation, as recorded after conduction, back to zero distance, where there is no dispersion of the axon potentials. In this way one obtains information forthwith about the whole group of five hundred or more fibers. The result of the procedure is apparent in Figure 5. At zero distance the duration of the delta group is the same as that of the alpha-beta group, about 0.5 msec. One could not let the matter rest, however, without recording the spike duration in single axons. When thus recorded the durations all fall between 0.4 and 0.5 msec., without systematic difference with respect to velocity (Fig. 6). Therefore, within the limits of the accuracy of measurement, in fibers in which the velocities range between 10 and 115 m.p.s., the spike durations may be considered as being constant.

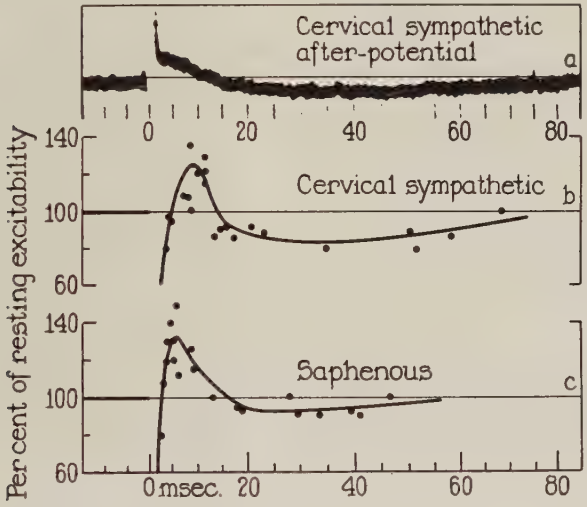


Figure 7. The after-potentials and excitability cycle of delta fibers. **a** and **b,** after-potential record and excitability cycle curve for the same nerve. **c,** excitability cycle curve for the delta fibers of the saphenous nerve of the cat. (Gasser and Grundfest, 1939.)

The refractory periods, on the other hand, vary in a continuous manner, as described by Blair and Erlanger for frog fibers. This observation was the occasion for considerable surprise, as no previous examples had been found of exceptions to Adrian's original finding that the absolutely refractory phase ends at the base of the spike. The variation of the refractory period is one of the legs of support of the contention that fibers vary to make a continuous series; therefore it demands special consideration. It is at this point that the usefulness of the after-potentials with their accompanying excitability cycles enters. For the refractory period has no greater significance in the characterization of fibers than have the after-potentials. And it may be said at once that the excitability cycles—and the after-potentials, where they can be recorded—are identical throughout the series. Figure 7 shows the

after-potentials and the excitability cycle in the delta fibers of the cervical sympathetic nerve of the cat, and the excitability cycle in the delta fibers in the saphenous nerve. They resemble their counterparts in alpha fibers. Some hitherto unsuspected variable must enter into the determination of the refractory period, probably the fiber size, as it also enters into the determination of the resting threshold of excitation. Support for this view is also found in Hursh's measurements on immature alpha fibers. In young animals, in which the alpha fibers are small, the refractory period is longer than it is in the adult. Taking into consideration all the evidence, the medullated fibers of mammalian somatic nerves may be regarded as constituting a homogeneous series.

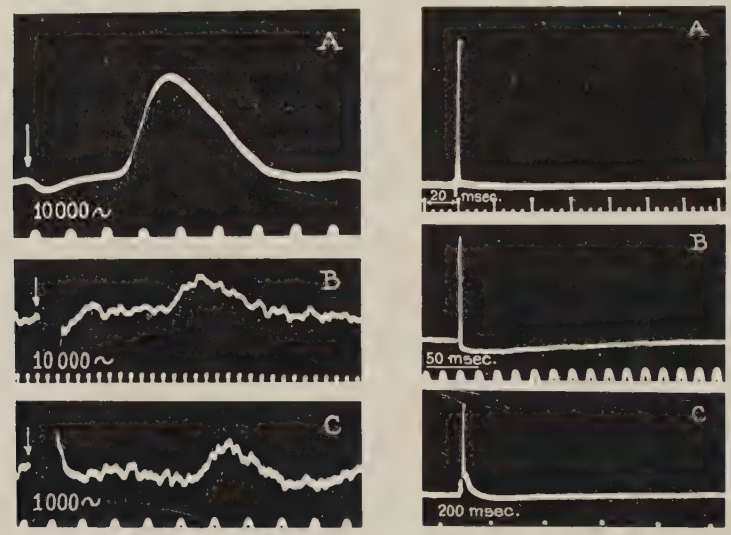


Figure 8 (left). Spikes recorded from unit axons of the A, B, and C groups. (See references 10 and 11.)

Figure 9 (right). After-potentials of the A, B, and C groups. The records are from multiple fiber preparations. (See references 10 and 11.)

In B fibers the spike, lasting about 1.2 msec., is longer than in A fibers (Fig. 8); and the after-potentials are in even greater contrast. Whereas the A fibers have a negative after-potential lasting about 15 msec., there is normally no visible negative after-potential in B fibers (Fig. 9), although one may be developed by special procedures. And whereas the positive after-potential in A fibers lasts only until about 70 msec. and in size amounts to only the equivalent of 0.1 to 0.4 per cent of the spike potential value, the B positive after-potential lasts 100 to 300 msec. and at its maximum has a size 1.5 to 4.0 per cent of that of the spike. The velocities found in B fibers range between 15 and 3 m.p.s. Thus, inasmuch as the slowest A fibers in the cat conduct impulses at about 10 m.p.s., there is an overlapping of velocities between

the two groups. Likewise there is an overlapping in the thresholds of excitation. The break between the two groups comes in the durations of the spikes and the characteristics of the after-potential; and it is obvious that neither of these features is tied to the velocity. In this connection it is interesting to recall that the delta fibers in the saphenous nerve of the rabbit, which are A in quality, have velocities in the range usually associated with B.

In the C fibers, which conduct impulses at velocities between 2 and 0.6 m.p.s., another sharp break in the properties occurs. The C spike lasts about 2 msec. (Fig. 8) and is followed by a negative after-potential lasting 50 to 80 msec. (Fig. 9). The latter in turn is succeeded by a positive after-potential traceable for 1 to 2 sec. Wherever the C fibers have been properly studied they have been found to be unmyelinated. And they are set off from other fibers in other ways, as for example in their high resistance to asphyxia.

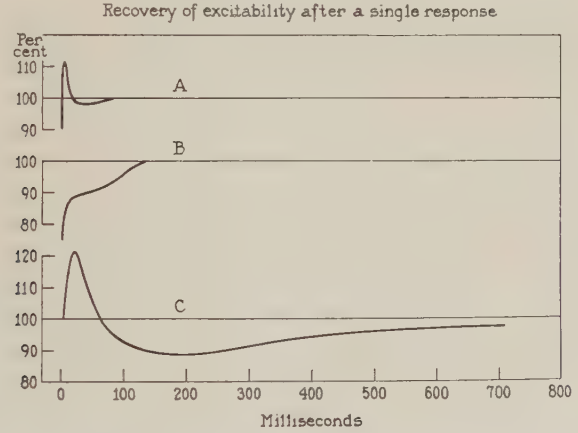


Figure 10. Course of recovery of excitability following single responses of A, B, and C fibers to excitation.

As a final point in the differentiation of fibers the course of their recovery of excitability following excitation must be mentioned. The excitability curves are quite characteristic and follow the configurations of the after-potentials (Fig. 10).

When all the data are tabulated it is apparent that while all velocities are present between the fastest and the slowest—between 115 and 0.6 m.p.s.—there is no corresponding variation in the properties. The fibers fall into three distinct groups with sharp boundaries. The classification of fibers made in this way, however, cannot be taken as the end of all classification. A number of observers have shown that there are large differences in the acetylcholine content of fibers—in the ventral roots as opposed to the dorsal roots, and in preganglionic fibers as opposed to postganglionic fibers. But these differences in metabolism do not reflect themselves in observations made with electrophysiological methods and they are part of another story.

With the confirmation of the validity of the division of fibers into groups, the way now became clear for the reinvestigation of the size-velocity relationship. Before entering upon a description of the final experimental drive made by Dr. Grundfest and myself, it will be necessary to mention two interim developments in order to fill in the picture of the background against which we were working. After observing a linear relationship between the spike size and conduction velocity in frog fibers, Blair and Erlanger reasoned that if the spike size is proportional to the axon area, as had always been held, the velocity must vary as the square of the diameter. Pumphrey and Young, on the other hand, concluded from observations made on velocities in relation to size in squid fibers that the velocity varies more nearly as the square root of the diameter. Even after due consideration is given to the difference between the two forms studied, the divergence of opinion inherent in these formulations is enormous. The correlating factor in one case is the fourth power of that in the other.

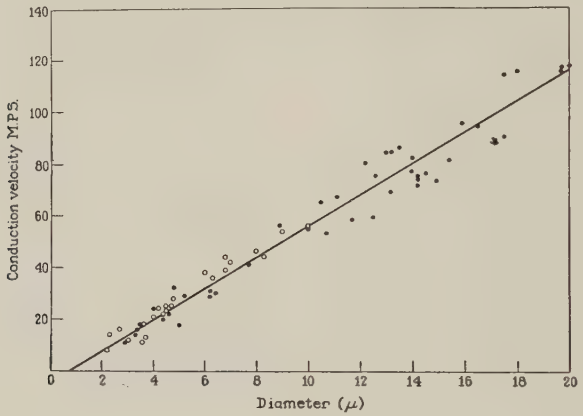


Figure 11. Velocities of conduction in the most rapidly conducting fibers of selected nerves, compared with the diameters of the largest fibers in those nerves. (Hursh, 1939.)

Before Pumphrey and Young's paper was published, Hursh in our laboratory was already making correlations between the maximal velocity and the size of the largest axon in mammalian nerves selected to yield collectively a wide range in diamaters. When the data were completed they represented velocities from 8 to 117 m.p.s., and the points connecting velocity to fiber diameter all fell about a straight line (Fig. 11). Not only did the data confirm the originally proposed diameter-velocity relationship, but they demonstrated its applicability at a range of velocities at which it had not previously been shown to apply. It may be asked, then, why the matter was not allowed to rest there and why we went on to the laborious reconstructions. The reason, as will soon become apparent, is that the reconstruction method affords a much more sensitive test of a velocity hypothesis.

Most of the observations were made on the saphenous nerve, usually of the cat, because of the well-marked elevations in the action potential with which the fibers may be fitted. After the action potential had been recorded and a map prepared of the distribution of the fibers according to sizes, it was possible from mere inspection of the map to make straight-away certain predictions about how the fibers would enter into the compound action potential. It can be seen in Figure 13 that the fibers fall into two main piles which should center on the alpha and the delta elevations. The delta elevation should start with fibers 3 to 4 μ in diameter; and, as the largest fiber in the nerve has a diameter of 14 μ and the factor relating the velocity of the fastest alpha fibers to that of the fastest delta fibers is approximately four, it follows that the delta elevation would be in the right place in the reconstruction.

After all the favorable preliminary indications it was surprising to see how poor were the first reconstructions made under the old rules. The delta elevation was about in the right place, but far too small. Numerous as were the small fibers, they did not supply nearly enough area to the end of the action potential. Another fault was that instead of a clean separation between alpha and delta, alpha crowded over and filled up the intervening space.

The most serious fault was the lack of potential area in the delta region—so serious that it revealed the fact that the assumption of the spike height varying as the cross-section of the axon must be incorrect. Almost every other part of the original rules had been questioned, rightly or wrongly. But it had occurred to no one to question this one, probably because it was hardly recognized that it was an assumption. It was based on the sound physical fact that the potential drop across a resistance, through which a current is flowing from a source that would yield the potential, E, on open circuit, depends upon the internal resistance of the source. As the resistance of the axons would vary as their cross-sections, this dimension was taken to be the controlling one in the calculation of the spike heights used for the first reconstructions; and, with the apparent success of the reconstruction of the early part of the action potential there was no reason for doubting its validity.

When once the difficulty was recognized, it was easy to see what the correct relationship must be. Blair and Erlanger, it will be recalled, had shown that the spike height in frog fibers varies directly with the velocity; and Zotterman had confirmed the relationship in mammalian fibers. Taken together with Hursh's demonstration that the velocity varies with the axon diameter, the correct interpretation of the observation of Blair and Erlanger is that the spike height varies as the diameter. Thus the sole support for the viewpoint that the velocity varies as the cross-section was removed. What had been neglected was the fact that the resistance of a nerve fiber depends not only upon its cross-section, but also upon a length. It has previously been pointed out that the spike durations are constant; therefore the wave length varies with the velocity, that is, with the axon diameter. Thus the proper statement about the internal resistance controlling the height of the spike is that the resistance varies directly as the diameter—because of the wave length—and inversely as the square of the diameter—

because of the effect of the cross-sectional area. The net variation, therefore, is inversely as the *first power of the diameter.* I will not bother you with the calculation of the spike heights when this variable is introduced. Suffice it to say that under the conditions obtaining in nerves, the spikes vary approximately as the axon diameters, as the experimental data indicate. It is the experimental fact, as illustrated in Figure 12, that I want to stress rather than the calculation.

With the needed potential area supplied, attention could be directed to other faults in the reconstructions. The alpha elevation was too broad and the alpha crest came too late. This fact meant too much temporal dispersion. Not only was all possibility that the velocity might vary as the square of the diameter removed, but linear variation itself appeared to be too great. And one thought of Pumphrey and Young's observations on squid fibers.

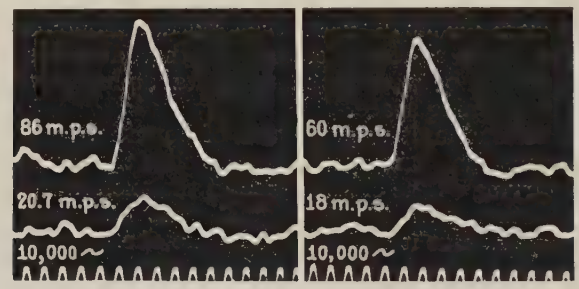
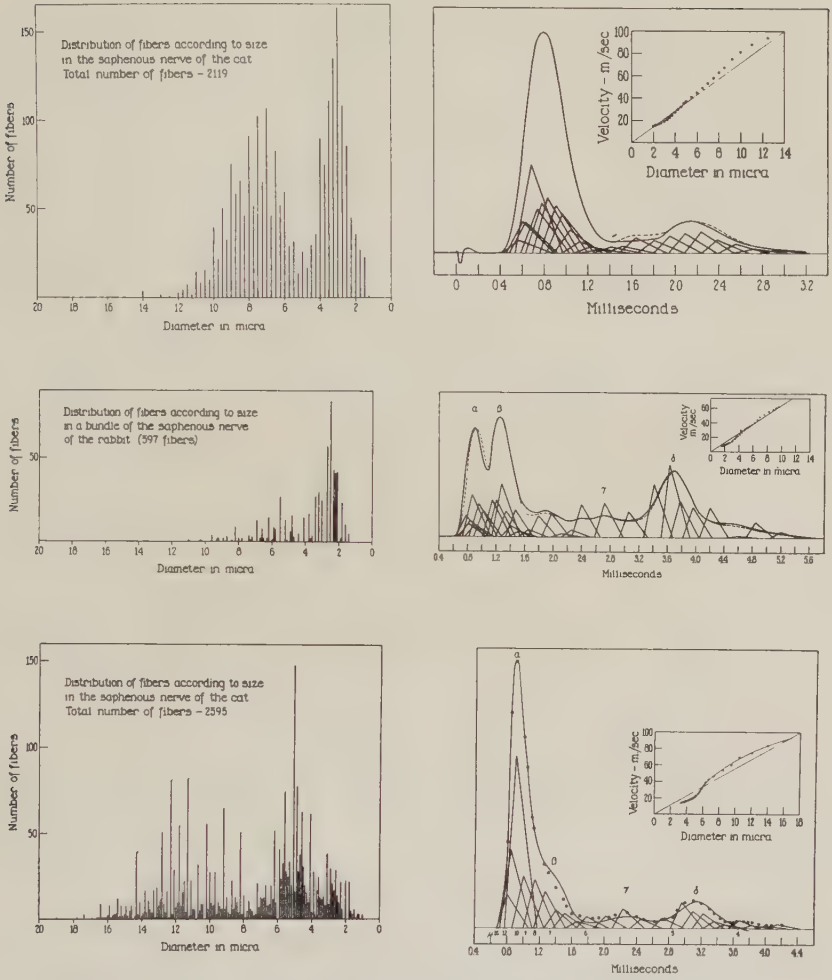


Figure 12. Comparison of the duration and heights of spikes in single axons conducting at different velocities in a branch of the saphenous nerve of the cat. The two groups are from different preparations. Left, $\text{velocity}_1/\text{velocity}_2 = 4.2$; $\text{height}_1/\text{height}_2 = 4.3$. Right, $\text{velocity}_1/\text{velocity}_2 = 3.3$; $\text{height}_1/\text{height}_2 = 3.8$. (Gasser and Grundfest, 1939.)

By now the correspondence between the recorded and the reconstructed potentials was so close that it was decided to change the plan of attack, in order to bring out wherein the discrepancies lay. It was decided to locate the fibers in the reconstruction in the right places, to cause them to make their proper contributions to the potential form, and then to calculate the velocities that would give them those positions. Thereby empirical velocity-diameter curves would be derived. In each instance excellent fits were obtained, as Figures 13 to 18 will show. The extreme sensitivity of the method will be noted. An error of a fraction of a micron in locating the slower fibers would throw their potentials grossly out of position. In each instance the same pattern emerges in the size-velocity curves. While their ends touch upon a straight line, the intermediate course is serpentine.

The next step was to account for the features of the size-velocity curves. The first question asked was whether any part of the curve was traceable to the fact that the outside diameters instead of the axon diameters had been used in the reconstructions. Use of the outside diameter is valid only in so far as its ratio to the axon diameter is



Figures 13–18. Distributions of fibers according to size and reconstructions of the action potentials from these distributions, shown for three different nerve preparations (Gasser and Grundfest, 1939). In the reconstruction curves the contour of the action potential as actually recorded is represented by a solid line. Where the reconstruction deviates from the record, the deviation is shown by lines made up of dashes or dots. Insets, corresponding size-velocity curves. Each dot in the curve represents a triangle in the reconstruction. Figs. 13 and 14 (upper). Saphenous nerve of the cat. Action potential record and reconstruction made for 4 cm. of conduction. Figs. 15 and 16 (center). Bundle ot the saphenous nerve of the rabbit. Action potential record and reconstruction made for 4 cm. of conduction. Figs. 17 and 18 (lower). Saphenous nerve of the cat. Action potential and reconstruction made for 6 cm. of conduction. In Figure 18 there may be seen the positions of the spike potentials in relation to the sizes of the fibers contributing them.

constant. A constant ratio was claimed by Donaldson and Hoke; but the more recent measurements of Schmitt and Bear and of Arnell are not in accord with their description. Arnell's data show that the myelin is relatively thicker on fixed mammalian fibers smaller than 8 micra. As the slopes of the velocity-diameter curves are greater below 8 μ, the observation appeared to be significant to our problem. If the fibers below that diameter have relatively thicker myelin sheaths, the fiber velocities determined by the axon would be slower than those indicated by the outside diameter and cause a depression in the outside diameter velocity curve.

We fortunately had in our possession a preparation of a fasciculus of the saphenous nerve containing 675 fibers, on which both the inside and the outside diameters had been measured. The ratios of the diameters were calculated. Above 8 μ the ratio was practically constant at 0.69, a value corresponding with Donaldson and Hoke's figure of 0.71. Below 8 μ the axon diameter outside diameter ratio fell off progressively.

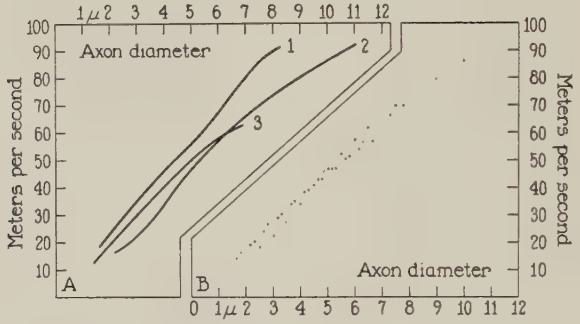


Figure 19. A, fiber diameter-velocity curves from Figures 14, 16, and 18 calculated in terms of the axon diameter and represented respectively in curves 1, 3, and 2. B, curves in A brought together by multipliers. (Gasser and Grundfest, 1939.)

With the aid of this curve, the size-velocity curves were recalculated in terms of the axon diameters, with the result that in two of the derivative curves the initial upward concavity disappeared, and in the third it was nearly obliterated (Fig. 19A). The three curves were then brought together by multipliers, in order to visualize the form of the axon-diameter velocity curve when freed from idiosyncrasies of the individual curves. While superficially the composite curve is linear, a close inspection reveals the fact that the points fall along a line having a slightly downward curvature (Fig. 19B). Whether or not this residual curvature is real cannot be stated. Some of the curvature can be accounted for on the basis of technical difficulties in measuring diameters, which I will not go into. And at times one gets perfect reconstructions of alpha spikes on the basis of a rigidly linear relationship between size and velocity. On the other hand, there is no theoretical reason why the graph should be a straight line, and in all probability it is a very flat curve approaching a straight line. Whatever deviation from linearity is

present causes the velocity to change more slowly than it would in strict proportionality to the diameter of the axons. But in any case, the deviation is negligible compared with that in the root functions proposed by Pumphrey and Young for squid fibers.

As the facts now stand, the velocity of conduction may be considered to be approximately in linear relationship to the diameter of nerve axons. The correlation is an empirical one and would apply equally well to any property of the nerve fibers which varies in the same manner as the axon diameter. With this statement we have the last entry in the log of the course taken in the solution of what at the outset appeared to be a simple problem.

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Elements of Genetics

Many students who are interested in human heredity are bored by extensive discussions of plant and animal genetics. The new book, "Elements of Genetics," is particularly well adapted to such individuals. Especial attention is paid to human traits, and an exceptionally long list is discussed at some length. The author is careful not to be dogmatic in his classification of the modes of inheritance of the traits discussed, and yet at the same time to avoid cumbersome technicalities.

Interactions of heredity and environment are ably presented in an interesting manner. Attempts to induce mutations in animals by feeding lead, alcohol and various chemicals are discussed. Comparatively little space is devoted to chromosomal aberrations and none to biometric techniques. The final chapter is an up-to-date discussion of eugenics. A glossary of genetic terminology is included.

The book is attractively bound and printed upon a good grade of paper.

—*D. C. Rife.*

Elements of Genetics, by Edward C. Colin. 386 pp. Philadelphia, The Blakeston Company, 1941. $3.00.

THE INTERACTION OF NEURONES[1]

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University of Chicago

That neurones interact is obvious from the simple consideration that each of you has several billion neurones in your cerebral cortex, yet remains a single personality. The general question I wish to raise is: How is this unification brought about? The existence of gross interaction is shown, more precisely, in many ways.

Lashley (1929) has offered impressive evidence of a mass function of the brain—not alternate to, but superimposed upon, its specialized local function—by studying the learning capacity of rats after the production of various brain lesions. The deterioration of learning ability he found to be highly correlated with the amount of cortex lost (r up to 0.86); but, since extensive criss-cross slicing of the whole cerebrum or removal of sufficient occipital lobe to destroy the same actual volume of cortex as destroyed by the cuts led to like learning losses; this did not correlate with the extent of interruption of recognized anatomical connections. What sort of neurone interaction might lead to this mass response?

Again, in the course of establishing a conditioned reflex, a particular afferent system comes to exercise control over an efferent oneup on which it normally has no action. In neurological terms, this means that two brain centers become able to interact physiologically as a consequence of having been repeatedly set into action together. How does the repeated ringing of a bell, when food is offered, open pathways between the auditory system and the salivatory nucleus?

Another form of interaction is manifested in the synchronized electrical beating of large numbers of neurones. This is widely manifest in neural masses—from the synchronized discharges of the uniformly illuminated retina (Adrian and Matthews, 1928), or the like impulse trains set up from the two respiratory centers and recorded in the phrenic nerves (Gasser and Newcomer, 1921), to the regular alpha rhythm of the human occipital cortex, and the equivalent regular beat of the isolated frog olfactory bulb (Libet and Gerard, 1939). How is this interaction achieved?

Closely related is the problem of the slowly spreading cortical waves seen in epilepsy or induced by convulsant drugs (Gibbs, Lennox and Gibbs, 1936; Adrian, 1936; Gerard and Libet, 1940). Even the well recognized dominance by more rostral neural masses, which check or suppress the activity of more caudal and phylogenetically older ones, presents a similar problem in interaction on a gross scale.

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At a finer level, a great mass of neurophysiological research has demonstrated in some detail the ability of one neurone to act upon another to change the state of the second (e. g. Symposium, 1939). This may be made to discharge and after-discharge or to cease action already in progress; its threshold may be lowered so that subsequent stimuli are facilitated, or raised so that they are suppressed; its potential may be shifted in the negative or in the positive direction; its metabolism may be increased or diminished. How are these effects brought about?

The mechanism of interaction, in this last case, is clearly that of synaptic transmission; and this of course analyzes further into chemical or electrical mechanisms. Some years ago (1932) I wrote, "Conduction along a nerve fiber involves excitation of a resting region by an active one, and both electrical and chemical components are present in the mechanism of propagation. At the ending, which is specialized, at least anatomically, either or both components might well be exaggerated to facilitate conduction over a critical region. Long enduring action or depolarization potentials or special chemical accumulation might equally well be utilized in various situations." To my mind, the enormous increase of information during the interim has not invalidated this position.

I do not propose to discuss the exciting controversy between those who insist on a material or humoral mechanism and those who equally insist on an energetic or electrical one. The chemical theories have faced a major difficulty, in accounting for very rapid changes, by emphasizing the appropriately high concentration of enzyme in junctional regions. The electrical ones have been similarly bothered by the problem of slow and enduring changes, and have interpreted these in terms of maintained interneurone bombardment and of long after-potentials. Since there is no anatomical basis for the former in autonomic ganglia, yet brief preganglionic tetany can alter the activity of ganglion cells for minutes afterwards (Bronk, Symposium), interneurone activity cannot be a universal explanation. On the other hand, it has long been known (Gerard, 1930), though often overlooked, that a few seconds tetanus may leave, even in nerve, considerable after-potentials which actually increase in magnitude during three or four minutes and endure for over fifteen.

Aside, however, from any chemical or electrical changes set up in highly localized fashion at a synapse, there is good evidence that each of these mechanisms acts more generally upon neurones, and independently of synaptic transmission. That the physico-chemical milieu of nerve cells can profoundly influence their activity or responsiveness, is now widely recognized. One need only recall, for example, the ability of an increased blood potassium concentration to arouse cats from anesthesia (Dubner and Gerard, 1939), or to triple the duration of the rebound limb positions following electrical stimulation of the deep cerebellar nuclei (Gerard and Magoun, 1936). I shall, therefore, in the remainder of this address, emphasize rather the electrical mechanisms which act grossly on the individual neurone and which are of prime importance in the interaction of the many.

Only in recent years has such non-synaptic electrical interaction begun to receive the attention it has long and obviously merited (e. g. Gerard, 1931). Now much evidence of its importance is appearing in the literature. Some examples are: the ability of a nerve action current to modify the excitability of a resting stretch of nerve even when the impulse with which the potential is associated is prevented by block from reaching this resting stretch (Hodgkin, 1937; Lorente de No, Symposium); the even more striking ability of the action currents from above such a block to re-initiate an impulse in the same nerve fiber two millimeters distant (Blair and Erlanger, 1939; Tasaki, 1939); the similar ability of the currents from one active nerve fiber to alter the thresholds of adjacent ones (Katz and Schmitt, 1940); and the tendency of separate axons in an isolated nerve (Adrian, 1930), of separated nitella cells lying in the same dish of water (Hill, 1939), and of individual spermatozoa clustered about a single egg, (Lillie, 1932), gradually to synchronize their rhythmic actions. I shall, however, base the further discussion on experiments carried out during recent years by Dr. Libet and myself on the isolated frog brain.

The frog brain is a peculiarly favorable preparation for study of the electrical activity of neurones. Its cells maintain the *in vivo* rhythm, some six beats a second of thirty microvolts amplitude, for several hours after the complete isolation of the cerebrum. Indeed, the potentials are commonly larger and more regular *in vitro* than they were in the same brain in the unanesthetized frog, exposed earlier under ether. Even a tiny bit of brain, as little as 1/10 of a milligram carefully teased from the olfactory bulb, can maintain its regular rhythm. Obviously, no circulation changes can confuse the picture, and the supply of oxygen and other substances by diffusion is adequate. It is thus possible to vary, in controlled quantitative fashion such conditions as temperature, salt or drug concentrations, or the like, while keeping other variables unchanged. It could be shown, for example, that a rise in temperature increases not only the amplitude and the frequency ($Q_{10}=2.3$) but also the regularity of the rhythm; while potassium increase, though accelerating the rhythm, soon disrupts it; and calcium, as usual, has the reverse action.

Further, the cells in the frog hemisphere are arranged in relatively simple patterns and form what amounts to a mosaic sheet near the ventricular surface. They are easily accessible to electrodes at either cell pole and thus, as we shall see, simulate the membrane of a nerve fiber studied by internal and external leads. Synaptic transmission in the isolated brain is retained under ordinary circumstances. Thus, brief tetanization of the olfactory nerve leads to an increase in amplitude of the olfactory bulb rhythm and to the appearance of waves at a higher frequency, and these changes may endure for several minutes.

Along similar lines, Mr. Tokaji and I have recently found that brief soaking of the brain in either acetylcholine or in eserine, at a concentration of 1 part in a hundred million, leads to a gradual increase (the maximum effect is not attained until a half-hour after the soaking) in the continuous activity and to the appearance of characteristic large diphasic repeated waves, Fig. 1. It is not yet certain, of course, that these drugs

act here to enhance synaptic stimulation, but their low effective concentrations, and the ability of nicotine to abolish their action, strongly suggests this.

Finally, the neurone mass in this preparation shows striking synchronization. That the few hundred or thousand cells in a single olfactory bulb are beating together is made strongly probable from the mere existence of the ordinary rhythm; for, if each cell were active independently of the others, a large, smooth and regular potential wave could not result. The synchrony is made quite certain when this ordinary rhythm can be altered, by appropriate change in conditions, so that regularly repeated waves occur at frequencies between one and fifty a second, at amplitudes from a few microvolts to over two millivolts, and with shapes from almost pure sine waves to highly skewed, humped,

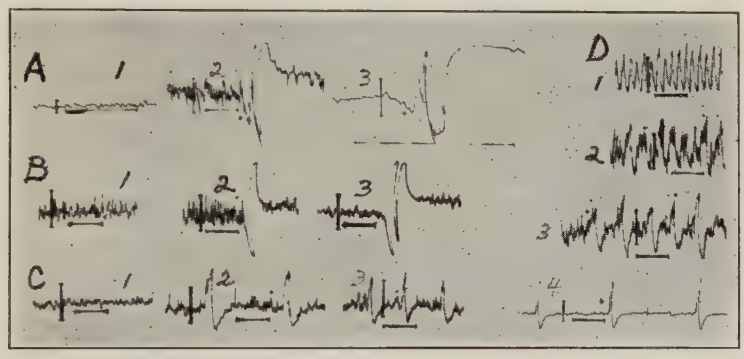

Fig. 1. Action of acetylcholine and eserine on isolated frog brain. Records in three horizontal groups (A, B, C) from three hemispheres, in vertical group (D) from olfactory bulb. Horizontal line = 1 second (read left to right), vertical line = 100 μV, except as indicated.

A 1. Normal (30μV); 2. 25 min. after 3 min. in 10^{-6}% eserine (HCl); 3. soon after 2, faster (300μV).

B 1. Normal; 2. 11 min. after 3 min. in 10^{-6}% acetylcholine; 3. 4 min. later (300μV).

C 1. Normal; 2. 24 min. after 3 min. in 10^{-6}% acetylcholine; 3. 9 min. later.

D 1. Normal; 2. 8 min. after 3 min. in 10^{-6}% acetylcholine (in serum); 3. 17 min. later; 4. 13 min. after 3 (300μV).

and even polyphasic, spike-like profiles. Though such irregular waves could be the resultant of simple waves of individual cells, so timed in their appearance as to sum to the recorded wave shape, this is *a priori* unlikely and only possible at all on the basis of recurrent excitation circuits. Yet nicotine, which blocks such circuits, still leaves very regular skewed waves.

Cell synchronization is, therefore, present and can profitably be studied in the isolated brain. Thus, greater regularity should denote more perfect synchronization, and it should be, and is, more difficult to disrupt a more regular rhythm than a less regular one by desynchronizing agents, such as potassium. By such criteria it has been shown

that synchrony is enhanced by an increase in temperature or calcium; by certain drugs, notably caffeine or nicotine; by a diminution of potassium or sodium; and, especially, by maintained constant currents.

The most useful property of this isolated brain, however, is its ability to generate slowly traveling waves; evoked especially conveniently by a brief soaking in caffeine. Following this treatment, there appear large surface-positive waves, of 0.1 to 0.2 second duration and one or two millivolts potential, each of which passes over into a surface-negative potential of lower amplitude and several times longer duration.

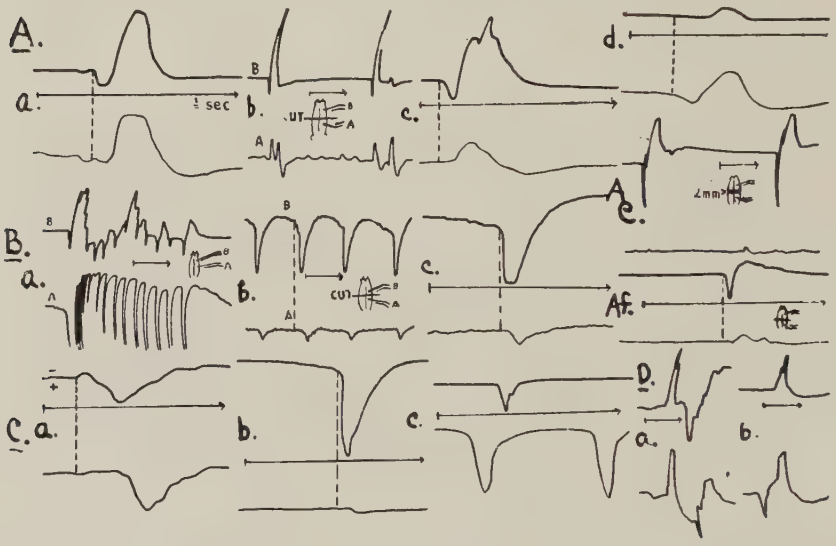

Fig. 2. Interaction across cut. Two channel simultaneous records.

A. a. Caffeine waves before cut; b. after complete transection across hemispheres, recording from each piece as shown; c. same later, showing front piece originating wave; d. still later, showing hind piece originating wave; e. pieces separated by 2 mm. (connected by Ringer's), note lack of interaction; f. pieces reapposed.

B. Another brain; a. caffeine waves before cut; b. after complete transection; c. same, faster speed, note that wave clearly spreads with finite velocity across cut.

C. Another brain; a. caffeine waves before cut; b. after complete transection between the two sets of electrodes; c. later, independent action of the two halves, showing non-interaction of recording systems.

D. Another brain; a. caffeine waves before cut; b. after cut.

The main wave, arising from a flat base line, is commonly followed by a train of satellite waves of progressively greater amplitude and lower frequency until the whole train stops. The entire sequence is repeated at regular intervals. Two channel recording shows that these caffeine waves travel over the hemisphere, most commonly in a rostro-caudad direction but sometimes in the reverse one, at the usual speed of 5 centimeters a second. (Fig. 2).

This slow propagation does not depend on synaptic excitation of successive cells, with or without interneurone circuits. The spreading caffeine waves are not altered by application of nicotine, which blocks synaptic responses, such as the on and off light response of the optic lobe, even in the presence of strong caffeine. Even more conclusive (since it might be argued that nicotine failed to block interneurone synapses which we could not directly test) is the finding that the caffeine waves can continue their longitudinal travel across a complete sharp cut made transversely through the brain at the middle of the hemisphere, providing the two brain halves are accurately reapposed. Separation of a fraction of a millimeter, even with Ringer solution in the

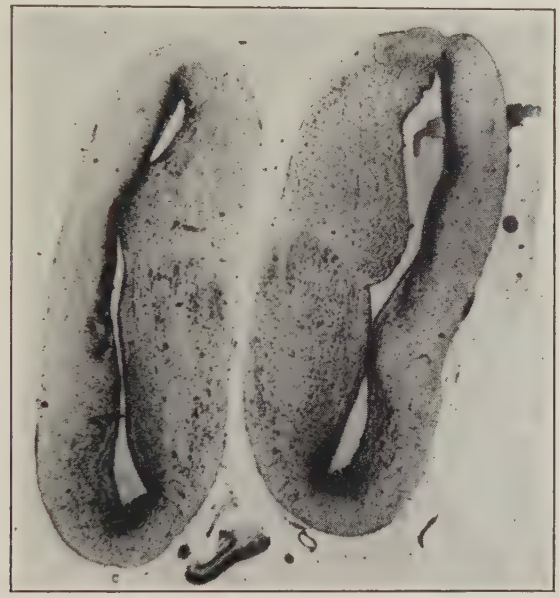

Fig. 3. Coronal section through frog hemispheres. Microphotograph ×15. Position of ventricular and pial electrodes indicated on right upper pallium.

gap, stops the wave at the cut; reapposition again allows it to travel from olfactory bulb to occipital pole, with no significant disturbance at the interposed cut. (Fig. 2).

Clearly, in this case, synaptic conduction is impossible; and a chemical mechanism cannot come in question. The probability was therefore strong that intercellular electric currents supply the mechanism for this wave propagation. If correct, it would follow that the activity of neurones in the normal brain, as well as in the caffeinized one, should be modified by passing appropriate constant currents through the brain mass—that is, by polarizing it—and, indeed, ascending or descending currents, of .05 milliamperes or less, do profoundly affect the electrical activity of the isolated hemisphere.

It will be useful at this time to present a theoretical interpretation in the light of which further data can be evaluated. The cerebral neurones, as can be seen in Fig. 3, form a sheet of closely packed cells near the ventricle and in a plane parallel to the pial and ventricular surfaces. Each cell is oriented with its dendrites towards the pia and its axon towards the ventricle. Let us assume that, in addition to the well recognized membrane potential, each cell is normally polarized along its perikaryon or soma, so that the dendritic pole is negative to the axonic. As seen in Fig. 4, the cell sheet would thus resemble a polarized membrane, as the nerve membrane, with an electric double layer. The postulated direction of the potential, as regards the outside and inside of the hemisphere is, of course, the reverse of that in the nerve membrane and, if correct, it should follow that an- and catelectrotonic effects produced by constant currents should also be inverted relative to the brain surface. We shall see later that this is the case.

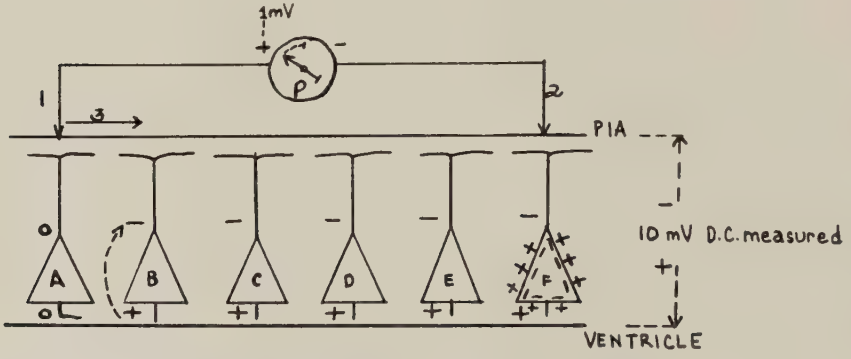

Fig. 4. Schema of cell layer in frog's cerebral hemisphere. See text. A caffeine wave is spreading as indicated by arrow 3 and has just discharged the somatic polarization of cell A. Cell B is discharging. The amplifier shows a pial surface positive wave of 1 mV. The usual interior-exterior polarization of the neurone surface is shown for cell F.

We postulate further that when the somatic potential is sufficiently decreased, that is when the axonic end of the cell moves in the direction of negativity relative to the dendritic, the cell becomes active and the somatic potential is discharged. Such a discharged cell, failing to oppose by its own potential the currents which tend to flow through and about it from the charges on neighboring cells, would act comparably to a depolarized region of the nerve membrane. The lowered resistance at this spot would permit adjacent somatic potentials to discharge, the neighboring cells would become active and depolarize, and a spreading wave of cell depolarization and activity would result. Similarly, one cell might actively send current through another with equivalent results. Since activation of one cell by another does not depend on synaptic transmission but on currents flowing through intercellular fluid, nicotine should not stop them, nor should a sharp cut providing the cut surfaces remain well apposed.

Many consequences of such a theory can be directly tested in terms of concrete predictions. For example, there should be a steady potential difference recorded between electrodes placed on the pial and ventricular surfaces of the thin hemisphere, the pial surface being negative to the ventricular. Measurements show a consistent DC potential, normally of 2–3 millivolts magnitude but with occasional much higher values, and usually in the right direction. The direction of this potential sometimes shifts spontaneously and can easily be altered by deliberate polarization across the thickness of the hemisphere. When traveling caffeine waves are then elicited, it is found, as the theory predicts, that the main wave has also reversed its polarity. In fact, as Fig. 5 shows,

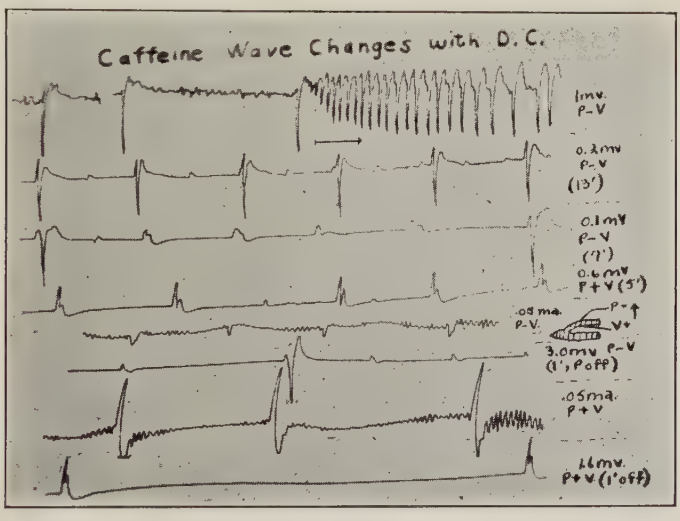

Fig. 5. Change in caffeine waves with P-V potential. From above down, time intervals between records are: 13 min., 7 min., 5 min. At 5th line, polarization is in progress as indicated, then 1 min. later. At 7th line reverse polarization in progress, then 1 min. later.

the direction and configuration of the caffeine wave correlates very well with the simultaneously measured P-V potential (pial-ventricular) as this slowly shifts in magnitude and direction.

The theory also predicts that the caffeine waves, as measured between electrodes on the pial and ventricular surfaces of the hemisphere, should be larger than those recorded between two electrodes on the pial surface, and should always be simple in form even when the latter show polyphasic variations. These predictions have also been experimentally confirmed, the P-V recorded wave being regularly larger, sometimes showing two or more times the voltage of the surface recorded wave.

Polarization through the hemisphere's thickness, ventricle negative to pia, would tend to depolarize the somatic potential, and therefore

should act comparably to cathodal polarization of a nerve. This it does, for it will regularly initiate waves in an otherwise inactive brain, and seems to cause the locus of origin of caffeine waves already present to shift towards or to the region of depolarization. "Anelectrotonus" has the inverse actions. Even the intensity and duration of the cell after-potentials are altered by polarization in a manner comparable to those of nerve.

It is thus obvious that this theory of somatic potential and intercellular electric currents, so closely analogous to the membrane theory of nerve conduction, serves well to explain the slowly spreading caffeine waves—as indeed it should, since it was devised for this purpose.

What is more important is its ability to explain other phenomena, as those of neurone interaction cited at the start of this address, without the necessity of introducing additional assumptions. Thus, for example, the spontaneous electrical beat recorded from brain neurones is probably a rhythmic variation of the somatic potential—indeed, if the membrane potential were to change simultaneously over the entire cell surface no external potential variation would appear—and the synchronization of the many beating cells follows simply from the above picture. Just as the current from a pacemaking nerve fiber or a nitella cell is able to sweep into unison with it other nearby units, about to fire off spontaneously in the course of their own rhythmic activity, so a pacemaking neurone (and not necessarily the same one at all times) would engage adjacent ones. Instead of having a slowly spreading wave, because the currents from one cell require a short time for their "detonator" action to stimulate the next, there would result an essentially simultaneous activity of adjacent units as their individual spontaneous rhythms fall into synchrony. The unifying action would spread rapidly to more peripheral units as the number of cells beating together increased and ever larger currents consequently flowed through the brain mass.

In the same way, by the interaction and summation of intercellular currents from large numbers of neurones, we can account for the phenomenon of a mass action independent of synaptic connections and for the existence of dynamic patterns of brain activity superimposed on, and partly independent of, the anatomical architecture. It is also obvious, I think, without developing the argument in detail, that the simultaneous activity of two nearby cortical regions, as in the course of conditioning, would alter the potential fields which would accompany the activity of either region alone and could so lead to the establishment of new functional patterns, of new conditioned reflexes. Finally, the somatic potential theory lends itself to a simple explanation of central inhibition which I shall shortly develop.

It will be desirable now to turn your attention again to the various interpretations of the functioning of the central nervous system which have been built up from the known properties of nerve fiber and synapse action, especially by Gasser and by Lorente de No. Gasser's theory of inhibition (Gasser, 1937), depending on the capture of an interneurone by one active neurone chain and so blocking transmission in a second chain to which it is also necessary, is familiar to you. I have dia-

grammed a slightly modified version of this in Fig. 6, which includes also a simple extension of the reasoning to account for the phenomenon of conditioning.

Of course, such nerve impulse theories fit admirably the phenomena of summation, facilitation, after-discharge, and the like—in connection with which they have been developed—and I daresay they could be extended to account for the phenomenon of synchronization, though this would certainly involve difficulties. But it is important to note that all such interpretations rest heavily on very precise structural relations between neurones, especially on the number and distribution of synaptic end-feet, and on the no less precise timing of the arrival of excitation from different sources so that they can or cannot sum their

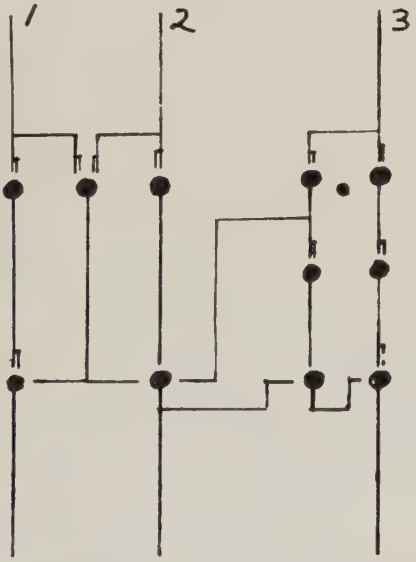

Fig. 6. Assume two synaptic endings on a neurone must act together to produce excitation. Then an impulse in afferent fiber 1 or 2 will excite its appropriate efferent. But 1 inhibits 2 by capturing the common interneurone. When 1 and 3 are active together, 1 can discharge the efferent neurons of 3.

effects, as the case may be. And, despite the clear experimental demonstration of many of these necessary conditions, there remain certain serious difficulties to face.

The facts outlined earlier, for example, that block of synaptic excitation by nicotine or of nerve fiber conduction by anatomical section do not abolish neurone synchrony or the spread of slow waves, are not reconcilable with pure nerve-impulse theories. Similarly for the equal loss of learning capacity, with equal loss of cortical tissue, with rat cortex destruction, independently of whether or not nerve pathways have been extensively interrupted. A further problem is encountered in interpreting the effects of influent nerve impulses

reaching different parts of a single neurose. It does not seem probable that groups of end-feet synapsing on widely separated dendritic branches can produce effects which interact, either for summation or inhibition, by any sort of membrane-propagated change along the neurone in question. Not only would a propagation of graded intensity, rather than of all-or-none character, be necessary, but also qualitatively different ones for excitation and for inhibition would be needed.

This latter difficulty would not arise if all the phenomena of inhibition could be accounted for by the shift of interneurones from one pathway to another. But such an interpretation does not seem able to account for all these phenomena. To take just one: ganglion cells, which are kept in a state of inhibition by maintained stimulation of inhibitory nerves to them, not merely fail to increase their resting rate of metabolism, but actually show a very considerable diminution in respiration (Dann and Gardiner, 1930). No type of theory which accounts for inhibition by any kind of increased activity, can be reconciled with these facts. Rather, each neurone itself, under the influence of whatever factors, must change its state in a direction inverse to that of excitation.

Finally, I must mention a body of data which throws some doubt on the interpretations of neurone function which require precise and set anatomical connections. Weiss (1940) has recently made separate implants under the dorsal fin of amblystoma of an extra leg and of a piece of spinal cord from another salamander. Ninety per cent of the neurones in the cord fragment disappear, and the remainder become completely disorganized by migration and growth of new processes. Dorsal column cells, for example, may sprout fibers which run out from the graft to form motor and sensory connections with tissues of the host and, particularly, with the neighboring limb implant. Yet, as the limb becomes innervated, it shows at first repeated generalized contractions, indicating synchronized discharges from many neurones, and later there appear well defined reflex responses which possess the usual attributes; of spacial and temporal summation, of gradation of response with stimulus intensity, of after-discharge, and the like. Inhibition has not been observed. The extent of synchronous action of these morphologically disturbed neurones is particularly well illustrated by implanting two legs on opposite sides of the cord section; for in such a preparation the two limbs always respond together.

In terms of the somatic potential, a theory of inhibition requires one essential assumption. If excitation follows the decrease or disappearance of this potential, inhibition should result when it is enhanced. Just as diminished polarization is associated with increased metabolism, increased polarization, produced from without, should lead to a decrease. We have in fact some evidence on nerve, although it is far from decisive, that a cathodally polarized region increases, an anodally polarized one decreases, its respiration. The further assumption needed is that those synaptic endings which excite a cell tend to be grouped at one pole, while those which inhibit it are grouped at the other. Then an identical action, such as the production of a local negativity, would, in the case of

an excitatory synapse oppose and so diminish the somatic potential, in the case of an inhibitory synapse sum with and so increase it.

To what extent such an anatomical disposition of functionally different endings does exist in the central nervous system is unknown, but that it can exist is clearly shown by the case of the Mauthner cell in certain fish brains. This large single cell, with a soma well over a millimeter long and two dendrites extending through the thickness of the tegmentum, receives synaptic connections of several well recognized types and from a number of known pathways (Bodian, 1937). (Fig. 7). End-feet on the axone hillock are of the small button type, come from fibers in the posterior longitudinal bundle, and are supposed to produce inhibition. End-feet on the dendrites are of the club type, come from the acoustic system, and are believed to cause excitation.

Fig. 7. Mauthner cell of the gold fish brain (from Bodian). Synaptic endings on the axone and axone hillock (above) are anatomically distinct from those ending on the soma or dendrites. This affords an anatomical basis for the type of inhibition here suggested.

The evidence, then, seems to show that nerve impulses traveling along definitive pathways are important in controlling the interaction of neurones, especially as they combine with one another in producing the special patterns of motor discharge and other fine regulations; and that many chemical substances, brought in the blood stream or formed locally, are likewise able to act upon neurones, regionally or generally, to modify their actions. But, in addition, there is the third factor, of electric currents flowing through and between neurones, which, perhaps more than either of the others, is involved in the interactions of nerve cells in larger groups and masses and which may also play an important role in certain of the more specific actions of one cell on another.

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Microbiology

Laboratory manuals in bacteriology differ principally in respect to the number of exercises, the order in which they are arranged, the introductory remarks to the exercises, and the clarity of directions. This manual is fairly complete, containing twenty-four studies, sufficient for a course in general bacteriology. The arrangement of the exercises may be questioned. In Exercise 4 the nitron cycle is diagrammed but nitrogen fixation is relegated to Exercise 19. Why the nitrogen cycle should be considered before and not as a part of bacterial physiology is difficult to see. Exercise 9 is on Typhoid and Dysentery in Water: Sewage is considered in Exercise 20. Exercise 12 in on Tuberculosis: Exercise 21 on Diseases of Human Beings. The introductory remarks are not without errors. Few will agree with the statement in the Exercise on Dental Bacteriology that *Streptococcus hemolyticus* is probably the most common organism in the mouth and that "carious and putrescent teeth may be a real predisposing cause of tuberculosis, as decayed teeth afford lodgment and a portal of entry for such microbes by way of the root canal." The exercises are well illustrated and the directions clear. At the end of each exercise is a list of pertinent questions and a list of references. The Appendix contains a glossary and directions for the preparation of stains and media. However, even though the errors in fact were overlooked, the arrangement of the exercises is such that it would be difficult to fit this manual into many courses in general bacteriology.

—*J. M. Birkeland.*

Microbiology Laboratory Manual, by Paul W. Allen and George M. Cameron. 243 pp. St. Louis, Mo., The C. V. Mosby Company, 1940.

ENCEPHALIZATION OF MOTOR FUNCTIONS DURING THE EVOLUTION OF THE PRIMATE NERVOUS SYSTEM

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I. INTRODUCTION

I had the privilege of spending part of August and most of last September in the gracious and hospitable atmosphere of Scandinavia, and since the visit was more prolonged than I had anticipated I put my time to good use by studying and collecting the works of that great Swede, Carl von Linné.

You are no doubt aware that he introduced the term "Primate," and since I was eager to learn how his concept of the first order of mammals had developed during the course of his scientific life, I traced the order through the various editions of his *Systema naturae*. The order is recognized in the first edition of the *Systema*—published in 1735 when Linné was 27 years of age—but under the name "Anthropomorpha," although the structural characteristics are not clearly defined. He merely described "dentes primores 4. utrinqu: vel nulli." Pectoral mammae and several other specific structural details are mentioned in the second (1740) and sixth (1748) editions,[1] but "Anthropomorpha" is retained as the name of the order, and it is not till the celebrated tenth edition of *Systema naturae* (1758–59) that the word "Primates" makes its appearance. Linné placed emphasis upon teeth as a basis of classification and definition of a primate from the 10th edition runs somewhat as follows:

"A quadruped with four parallel incisors, single canines, two pectoral mammae, hands rather than paws, two complete clavicles and an arboreal habitat."

Linné included the bat in his original classification and his definition of the order would also have embraced many related forms, such as the flying lemurs, tree shrews, etc. The *Bradypus*, for example, were included in the first, second and sixth editions, but they were dropped from the Primates in the tenth edition and in the twelfth.[2] To the Linnean characteristics, one nowadays, in defining the primate, adds that it has five fingers and five toes, usually flat nails, the first and second digits being opposable; the thumb and hallux may be atrophic. Usually a single offspring is produced at birth in a completely helpless condition, but twinning occurs normally in some of the lower primates, and multiple birth may rarely occur in all forms.

[1]The only editions of *Systema naturae* prior to the tenth that Linné himself revised.

[2]The twelfth edition was in part revised by Linné, and was the last edition that he touched.

I cannot here go into Linné's subdivisions of the primates, but let me briefly remind you that one now recognizes three suborders of primate, the *Tarsioidea, Lemuroidea* and the *Pithecoidea.* Their characteristics are as follows:

Tarsioidea. The group of animals nearest the stem of the primate tree are believed to be the tarsioids which are represented by only one existing species, *Tarsius Storr.* Recent studies of Matthew (1928), Chester Stock (1938) and others, indicate that tarsioids similar to existing species were found in the middle Eocene, and that they flourished then in this hemisphere and in Europe, as well as in the Orient. At present they occur only in a limited part of Melanesia, namely the southern Philippines, the Celebes, Northern Borneo, the Malay peninsula, and possibly in some intermediate islands. Few, if any mammals, other than *Tarsius,* have survived from the middle Eocene and hence they must be regarded as among the oldest existing mammals—they are indeed "living fossils."

Interest in the comparative study of cerebral function prompted me two years ago to make a trip to the southern Philippines to study the *Tarsius* with a view to exploring the feasibility of transporting them to this country by air (Fulton, 1939). Tarsiers had not hitherto been brought either to America or to Europe, although the attempt had been made on several previous occasions. Too little was known of their feeding habits, and of their uncertain temperament. While in the Philippines I made the acquaintance of a retired army captain, Mr. Norman Cook, who, while stationed in the Davao Gulf in southern Mindanao, had succeeded in keeping tarsiers as pets and he passed on to me his notes concerning their feeding habits and other features of their natural history (see Cook, 1939; see also Lewis, 1939).

Among other things Captain Cook's notes indicated that tarsiers would eat only living food, and, as had long been suspected, he found that they were primarily insect-eating. Profiting by this information, I succeeded in keeping a number of specimens alive and transported one by Clipper back to Honolulu, but in the old clippers odds were against one because livestock had to be carried in unheated baggage compartments which at 12,000 feet frequently fell to a subfreezing temperature. I made arrangements, however, with an enthusiastic young naturalist named John Eckman to bring back some specimens by boat and these arrived in November, 1938. A pair, male and female, have survived for eighteen months in my laboratory (Catchpole and Fulton, 1939).[3] These are, I believe, the first tarsiers to be maintained in captivity outside of Melanesia. The male is just becoming sexually mature; the female's sex cycles have been closely studied, but she did not reproduce. It is of some interest that this specimen of *Tarsius* has proved to have quite regular 26 day cycles (oestrus).

The morphological characteristics of the tarsioids indicate that they occupy a place of transition between the insectivores and the primates. Hence, a study of their brain from the structural as well as from the

[3]Both animals died quite suddenly of filarial infestation in June and July, 1940. some twenty months after reaching this country.

functional standpoint is of the greatest possible interest (see Woollard, 1925, 1935; also Woodward *et al.*, 1919).

Lemuroidea. An offshoot of the primate stem is found in the lemurs, galagos, pottos, aye-ayes of Central Africa and Madagascar which answer to Linné's definition of a primate. They are less significant from the point of view of the primate evolution than are the tarsioids, because they probably represent an offshoot considerably distant from the base of the primate tree. However, they are more available than are the tarsioids and exist in a great many species.

Pithecoidea. An enormous branch of the order of primates is grouped under the pithecoids which include two large divisions (i) the Old World Monkeys (catarrhines) including all the apes and man and (ii) the New World Monkeys (platyrrhines). Hence, from the point of view of comparative study of the brain, the suborder Pithecoidea includes those forms to which attention is ordinarily directed. The grouping within the three suborders is indicated in the following table:

ORDER I: PRIMATES

I. Tarsioidea, a rare insect-eating primate which has changed little since Eocene times and exists in only one Genus: *Tarsius* Storr (several species or varieties). They are nearer the base of the primate stem than any other extant form.

II. Lemuroidea, a lowly offshoot of the primate stem, with tarsioid affinities, exist in four families:

1. *Lemuridea*.....Lemurs.
2. *Lorisidea*.....Loris, Potto.
3. *Galagidea*.....Galago ("Bush-baby").
4. *Daubentonudea*.....'Aye-aye."

III. Pithecoidea, an enormous group including Old World (*Catarrhini*) and New World (*Platyrrhini*) monkeys, the anthropoid apes and man, divided in six families:

Monkeys

(*Platyrrhini*)

1. *Hapalidae*.....Marmoset.
2. *Cebidae*.....Ring-tail, Spider, Woolly, Howler.

(*Catarrhini*)

3. *Cercopithecidae*.....Langur, Four-fingered, Green and Red Military Monkey, Macaque, Japanese Ape, Baboon, Mandrill.

Anthropoid Apes and Man

(*Catarrhini*)

4. *Hylobatidae*.....Gibbon.
5. *Pongidae*.....Orang-utan, Chimpanzee, Gorilla.
6. *Hominidae*.....Man (only one existing species).

II. THE COMPARATIVE APPROACH

Marshall Hall (1833) insisted that the nervous system is to be regarded as a group of segmental reflex arcs which had become functionally interrelated in the course of evolutionary development, the headward segments having become dominant over the segments more

caudally situated. The most conspicuous feature in the evolution of the brain, especially of primates, lies in the growing dominance of the cerebral cortex over all lower levels of nervous function.

Evidence of this dominance has been inferred from the increased complexity of the anatomical matrix in man and chimpanzee, as compared with pithecoid monkeys and lemuroids; but complexity of the matrix has of itself little meaning in the absence of functional analysis. From the response to *stimulation* important indications have been obtained concerning functional complexity. The exposed brain of various animals had been stimulated in 1800 by Aldini (1804), during the controversy which followed the discovery of animal electricity (1791), but the motor area as such was not disclosed. The German neurologist, Hitzig (1874), was the earliest to stimulate the motor area of the monkey and to compare his results with those obtained in the dog, but he did not compare the monkey with other primate forms. An abortive attempt in this direction was made by Beevor and Horsley in 1890, but the first systematic comparison of monkey, orang, chimpanzee and gorilla, was made by Sherrington and his collaborators between 1892 and 1917 (see especially Leyton and Sherrington, 1917). Cushing (1909) and Foerster (1936) later extended corresponding studies on responsiveness to electrical stimulation to the human brain (see also Penfield and Boldrey, 1937).

Another functional approach, more revealing than that of electrical stimulation, lies in comparative study of the effects of ablation of corresponding areas of the brain in different primate forms. It was David Ferrier (1875) who first proved in the monkey that if a region excitable for the arm is removed the arm becomes paralyzed. Leyton and Sherrington (1917) made a similar observation in the chimpanzee, and they imply that paralysis was more profound relatively in the chimpanzee than in the monkey when a homologous area was removed; no emphasis, however, was placed upon the more enduring character of the paralysis in anthropoid as compared with monkey.

In recent studies begun late in 1930 with Allen D. Keller (Fulton and Keller, 1932) and since continued over a period of ten years with a series of collaborators, we have had opportunity to make a systematic comparative study of the effects both of stimulating and of ablation of some forty different species of primates, beginning with pottos, galagos and marmosets, and extending through old and new world pithecoid monkeys, four orangs and some 80 chimpanzees. More than two thousand pithecoid monkeys have been used in the course of the study.

Evidence of Encephalization

The most primitive nervous system, even that of the earthworm, is organized in terms of functional levels, and it is obvious that the more headward levels are dominant over the more caudal segments. The extent of this dominance, however, varies widely in different species, and it is for this reason that much importance is attached to the comparative physiology of the central nervous system. Such comparative studies have progressed in two important directions: (i) analysis of the gradual encephalization of function, and (ii) investigation in a given

form of functional localization in the cerebral hemisphere. The last phase of the problem will be touched upon at the end of this discourse.

Motor systems. An illustration of differing degrees of dominance of the headward segments is found by comparison of cat with monkey. The cat (or dog) after removal of its cerebral hemispheres exhibits essentially normal locomotor movements; it is able to walk and to maintain itself upright against the force of gravity. An adult pithecoid monkey, however, when it loses its cerebral hemispheres, never regains its ability to walk; in other words, the control of locomotor movement has; in these primate forms, become almost completely taken over by the cerebral cortex. Locomotor function has become, as we asy, "encephalized."

There are certain relatively constant features of organization of the brain in all primate forms. The first is the position of the motor and sensory areas. In pithecoids the cerebral hemisphere is divided by a fissure, usually referred to as the "central sulcus," which separates the rostral (motor) from the caudal (sensory) portion ot the hemisphere. In some of the Lemuroids there is a small dorsal sulcus that sometimes unites with sulcus rectus to form a primitive central sulcus (Connolly, 1936, p. 307). In *Tarsius* the hemisphere is usually quite smooth, but occasionally in *Tarsius*, as in the marmosets, there is a slight indentation coinciding with the posterior margin of the motor area (Woollard, 1925). The posterior division of the cerebral hemisphere, *i. e.*, the part lying caudal to the central sulcus, is primarily sensory in function and receives the great sensory projections from the thalamus and from lower spinal levels. The frontal lobes constitute the anterior portion of the hemispheres and include all tissue lying rostral to the central sulcus. This part of the hemisphere is primarily motor in function, but it also has a vast assemblage of interneurons which increase enormously in extent as one ascends the primate scale. The fore part of the frontal lobe is made up almost entirely of interneurons, and the region itself is referred to as the "frontal association areas." They are primarily concerned with higher intellectual functions, *i. e.*, memory and the capacity to plan for future action.

How does one know that the brains of chimpanzee and man are more encephalized than those of pithecoid monkeys, lemuroids and tarsiers? A suggestion comes from stimulation of the frontal lobes. The motor area of a tarsier has never been stimulated—the animal is still too rare and too precious—but I have stimulated pottos and galagos, which belong to the lemuroids, and also marmosets, and there are, in addition, several reports of stimulation of prosimiae in the literature (Volsch, 1906; Mott and Halliburton, 1908). It is strikingly true that only the most stereotyped movement patterns can be evoked from the central cortex of these primitive primates, whereas in chimpanzee and man highly discrete movements of individual fingers, corner of the mouth, the eyelids, the vocal cords and other individualized movement patterns can be evoked on cortical stimulation. Moreover, in man and chimpanzee there is a mosaic of sharply circumscribed foci controlling these specialized movements; while in the lemuroids the distribution of excitable points is homologous, but excitable foci are much less individualized.

The evidence of encephalization becomes much more impressive, however, from study of the effects of isolated ablation of those areas in the frontal lobe which an excitation gave movement, *e. g.*, of the leg. If the leg area is removed, the leg itself becomes paralyzed. *The extent and duration of the paralysis, however, varies widely in different forms.* It was mentioned that a cat, after complete removal of the hemispheres, is able, after a period of several hours, to walk about as if nothing serious had happened. The galago, potto and marmoset behave much as would a cat, although they exhibit a somewhat more enduring paresis. Mott and Halliburton (1908) were also struck by the slight character of the paresis following motor area ablation in the lemur. On removal of the leg area of a galago or potto, the leg shows obvious weakness for a few days, but power is regained after a period of time and the animal ultimately progresses as if nothing had happened. Pithecoid monkeys, such as the macaque, exhibit a profound paralysis when the foot area is removed, but recovery gradually occurs and after a few months the animal may move its foot almost normally in ordinary locomotor movements (see Fulton and Keller, 1932); signs of weakness, however, persist indefinitely in circumstances of fatigue, for even six months or a year after destruction of the leg area an animal will begin to drag its affected foot after a fatiguing chase. Hence, the mechanism governing foot movements are sufficiently encephalized in the macaque monkey to give some degree of *permanent* deficit when the foot area is removed. The baboon is considerably more affected than a monkey, and the gibbon lies clearly between the baboon and chimpanzee in intensity of its cortical paresis. Turning to chimpanzee and man, a far more profound paralysis results than in pithecoids or in the gibbon, when the foot area is ablated, *i. e.*, both chimpanzee and man exhibit a permanent and readily recognized motor deficit when the foot area of the frontal lobe is destroyed.[4]

If one compares the hand instead of the foot, the difference between species is even more striking, for a human being whose arm area has been destroyed, can never again use his fingers for the fine movements essential to play the piano, or even to button a shirt. Monkeys, on the other hand, although they do not ordinarily play the piano, exhibit other exquisitely delicate movements of the fingers and these show far less ultimate impairment following a lesion of the arm area than those of chimpanzee and man. Hence, we are led to conclude that the patterns of skilled movements are more highly encephalized in man and ape than in monkey.

In passing, it is interesting to note that control of movements of the tail in certain prehensiled tailed South American monkeys is so completely encephalized that when the tail areas are removed bilaterally, the tail itself becomes permanently and completely paralyzed, exhibiting only a spastic prehensility similar to the condition of spasticity encountered among primates after decerebration (Fulton and Dusser de Barenne, 1933). Human tails occur atavistically and some have been motile, implying cortical representation (Ross Harrison, 1901).

[4]These comparisons, especially among the prosimia, are based upon unpublished observations. For the pithecoid monkey, baboon, gibbon and chimpanzee, see Fulton and Keller, 1932.

Sensory systems. One may cite many parallels in the sensory sphere of similar encephalization of function. One of the most striking is that of the visual system. In fish, the optic system appears to be without significant connection with the forebrain and removal of the cerebral hemisphere causes no obvious impairment of vision, although behavioural disturbances are said to follow (G. K. Noble, unpublished). According to Schrader (1889), much the same is true of reptiles and birds. However, in rodents, particularly rabbit and rat, the visual cortex becomes encephalized; if the occipital lobes are removed, pattern vision is impaired, but the capacity to discriminate between differing intensities of light still remains unaffected (Lashley, 1932). Marquis (1932, 1938) has shown that dogs appear for a time completely blind after removal of the occipital lobes, but that brightness discrimination eventually returns with little or no impairment, while object vision is entirely destroyed. In monkeys object vision and brightness discrimination disappear entirely; a considerable degree of brightness returns (Malmo, unpublished). Man is rendered completely and permanently blind by extensive injury of occipital lobes, and he regains no consciousness whatsoever of light when this part of this cerebral hemisphere has been destroyed.

The encephalization of other categories of sensory functions follow a parallel schema, notably in somatic sensation in relation to the parietal lobes (see Ruch, 1935, and Ruch, Fulton and German, 1938).

When one approaches a given function of the human brain from the comparative standpoint by studying the particular function in a series of animals extending from tarsier and the lemurs up through the monkeys and the great apes, one can "extrapolate" quite accurately and predict how man will defer in regard to this particular function.

So much then for the principle of encephalization. Clinical neurologists often remark: "Well, you are working on cats and monkeys and your results are, of course, not applicable to the human being." My reply to this is generally somewhat direct, namely, that, if one approaches human function from a comparative standpoint far more basic light can be thrown upon it than by concentrated studies carried out on man himself without reference to his forebears in the evolutionary scale. A study of the monkey is also quite meaningless so far as the rest of the animal kingdom is concerned, unless a given function in one species is compared with the corresponding studies on forms occupying differing positions in the animal scale. The comparative approach to the human brain explains why it functions as it does.

III. FUNCTIONAL LOCALIZATION IN THE FRONTAL LOBES

The greater part of the cerebral cortex is made up of six primary layers of cells, but each layer has a different *cellular architecture.* The frontal lobes are subdivided on the basis of cytoarchitecture into a number of structurally discrete fields to which Korbinian Brodmann (1909), the Armenian histologist, gave an erratic series of numerical designations. Thus, the motor area—which on stimulation causes movement of skeletal muscles—is known as area 4; the adjacent premotor region as area 6; another area which on stimulation moves the

eyes is numbered 8, etc. The map in Fig. 2 gives these numerical designations as modified by Dusser de Barenne; the capital letters L, F and A denote respectively Leg, Face and Arm, so that area L.4 is the leg area and A.6 the part of the premotor area concerned with the arm, etc.

(Motor fields (Areas 4 and 6)

The excitable characteristics of these areas has already been described, *i. e.*, a mosaic of discrete foci can readily be demonstrated. When these areas are ablated in monkeys or chimpanzees, an enduring paralysis occurs; indeed, if areas 4 and 6 (including leg, arm and face) are destroyed bilaterally in an adult monkey, the animal is as gravely paralyzed as when both cerebral hemispheres are removed (Bieber and Fulton, 1938). This means not only that the motor functions are encephalized to this surprising extent in higher primate forms, but it also indicates that they are *localized* to a given rather small area within the cerebral hemisphere. This localization is far less discrete in the lemuroids than in the pithecoids.

In the adult pithecoid the functional localization of motor patterns is so complete that enduring volitional paralysis follows bilateral ablation of particular regions. But this is not true of young animals of the same species. You are familiar with the biological concept that ontogeny tends to repeat phylogeny, *i. e.*, that embryological development is on its broad outline a recapitulation of evolutionary history. It is undoubtedly, therefore, a fact of prime importance that when the motor and premotor areas are removed from monkeys shortly after birth, as has been done in the recent studies of Dr. Margaret Kennard (1938), the baby pithecoids behave much as do *adult* galagos and pottos after a similar lesion, *i. e.*, they have only slight motor paralysis. However, as these baby macaques grow older, signs of deficit begin to appear; but they never become as grave as the paralyses which follow a corresponding ablation in an adult animal. There exists in the infant nervous system of a pithecoid monkey, greater capacity to reorganize its functional localization, *and the pithecoid infant behaves as if it were an adult lemuroid.*

Dr. Kennard is much interested at the moment in attempting to discover what part of the nervous system is responsible for integrating movement patterns of her normal infant macaques. The basal ganglia undoubtedly play an important role; but during the first six months of life their function is gradually taken over by the cerebral cortex. In these young animals, therefore, as in the human infant, the evolutionary process of encephalization proceeds under our very eyes.

Considerations of space forbid more detailed discussion of the other cytoarchitectural areas of the cerebral cortex, but in the case of all those which have been fully investigated a corresponding increase of functional discreteness has been established as the primate scale is ascended. In the tarsioids and lemuroids the cerebral cortex is smooth and only the major fissures—such as the Sylvian—can be identified; the boundaries of lemuroids are more indefinite functionally and anatomically than in the pithecoids. The insectivors and rodents have a similarly smooth cortex with even less discreteness of functional localization, and this has no doubt been responsible for a modern error among

experimental psychologists who, until very recently, have insisted in the equipotentiality of all regions of the cortex. In so far as "learning" is concerned there may be a basis for their contention—and this is true of man as well as animals—but when one scrutinizes the great sensory and motor functions of the primate forebrain the concept of equipotentiality is not only one of harmony with every known fact of comparative neurophysiology, but it is in addition naive and misleading.

The functional approach to the evolution of the primate brain has thus given clarity and precision to doctrines which in the past have been based largely upon inferences drawn from morphological studies.

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A SCALED MODEL OF A PROPOSED PROTEIN STRUCTURE[1]

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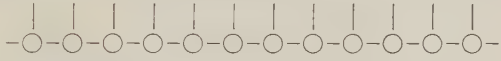
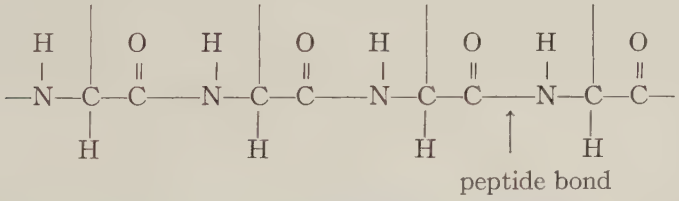
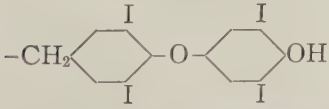
This little article is intended to give a brief view of our present quite imperfect picture of protein molecule structure, and is addressed particularly to some of the geometrical aspects of the situation.

In a certain sense it is possible that the structure of the protein molecules is very simple. According to the classical theory, based largely on Emil Fischer's work, a protein molecule is a chain-like structure, the nature of which may be indicated in the following manner:



where the members of the chain are amino acid residues. The small circles, or heads, are the same for all amino acids (we shall pass over the imino acids). They are joined together by the "peptide" bond, formed by splitting off water between the –COOH group in the head of one amino acid and the $-NH_2$ group in the head of a neighboring amino acid, thus:



The tails, or side chains, are different for different amino acids. For glycine, the side chain is –H; for alanine $-CH_3$; for lysine $-CH_2CH_2CH_2CH_2NH_2$; for tyrosine ; for thyroxine  ; etc. About twenty-four different amino acids seem to be important in animal metabolism, although a few others are known.

[1]The model described here was first presented at a Symposium at the Richmond Meeting of the American Association for the Advancement of Science in December, 1938; and again at the Columbus Meeting of the Ohio Academy of Science in May, 1940.

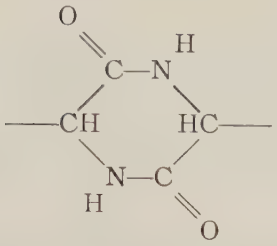
In another sense of the word, protein structure may be considered as not at all *simple*. The average molecular weight of the amino acid is about 120. Since the molecular weight of various proteins range from perhaps about 34,000 up to 100,000,000 or more, it is obvious that a very large number of amino acid residues are present in such giant molecules. It has been suggested that the many shades of physical and chemical properties, which the proteins are known to possess, are to be accounted for not only by the actual total number of amino acid residues present, and by the particular kinds of residues present, and by their relative population but also by the nature of their sequence along the molecule backbone. A chain –GGGAAAGGGAAA–, where G and A represent glycine and alanine, might well produce an entirely different set of behaviors than the arrangement –GAGAGAGAGAGA–. With only a few different amino acids in a backbone which is merely a few hundred links long, the number of possible permutations is, of course, immensely large. It seems likely, too, that a regularly repeated order of arrangement would lead to quite different properties than a random one.

Bergmann (1) and others have, in fact, shown that the amino acids are probably arranged in some definite order, in natural protein molecules, and in some cases it has now been possible to deduce the sequence. "Living organisms therefore do not achieve the synthesis of the immense number of proteins provided by the peptide theory in its original conception, but seem to synthesize only those proteins that exhibit—simple numerical rules. The discovery of the quantitative rules governing the protein molecule makes the biological synthesis of an individual protein molecule appear as a process which involves a specificity that is both highly delicate and extremely complex. Such specificity phenomena are a clear indication of the operation of an enzymatic process which directs all the steps involved in the synthesis of the special pattern of each individual protein."

STRING, SHEET AND BODY STRUCTURES

There is reasonably good evidence for the conclusion that some protein molecules exist as strings, others as sheets or as 3-dimensional lumps of some sort. It is not unlikely that a given molecule may assume all of these shapes in different settings. Long ago, for example, Dr. Nouy (2) estimated the size and shape of certain protein molecules lying in a water surface, and concluded that they were tiny cylinders or prisms, probably formed by the coiling up of the long string-like molecules. Mirsky and Pauling (3) have pointed out that the well-defined properties of native proteins require that their molecules have definite configurations. Whether such protein molecules, lying alongside one another, are joined together laterally by chemical bonds (somewhat after the manner of vulcanized rubber molecules), or by hydrogen bonds, or by van der Waals forces, strong or weak, is a question to which we would like to have an unambiguous answer.

In this connection, an extremely interesting theory has been advanced by Dr. Wrinch (4)—the cyclol fabric. It is supposed that two amino acid molecules unite to form a closed diazine ring, by splitting off water as in the formation of the peptide bond:



The formation of such a hexagonal ring is plausible. Indeed, if the two side chains are H atoms, this diazine ring is diketopiperazine, which is known to exist. Corey (5), by X-ray examination of the crystal, has found that the diketopiperazine rings are flat, and that they are joined together by hydrogen bonds in long strings.

Now, according to the early Wrinch theory, these diazine rings unite chemically with one another by the reaction

$$>C=O+H-N<\longrightarrow>\overset{\overset{OH}{|}}{C}-N<$$

to give a structure, in which three diazine rings meet in a triazine ring, and which by extension in space yields the so-called cyclol fabric (Figure 1) a sheet-like structure. Further, it is supposed that the fabric can fold into a "cage," which is a truncated regular tetrahedron. Pictures of the model of this structure are shown in some of Dr. Wrinch's papers, but will not be reproduced here. The smallest cage of this type contains 72 amino acids, and the larger ones $72x2^2$, $72x3^2$, $72x4^2$, etc. Since the average molecular weight of amino acids is about 120, the molecular weights of these protein cage molecules (forgetting the smallest) would be about 34,000, 76,500, 136,000, etc. This seems to be in remarkably close accord with the actually observed non-random distribution of molecular weights; although an alternative explanation which has been offered is that chain molecules of certain definite lengths, with none in between, may be formed because of the nature of the act of protein synthesis.

SCALED MODEL OF CYCLOL FABRIC

While, as already stated, the formation of the diazine rings is plausible, a very serious difficulty confronts the hypothesis that these rings can join together to form the fabric. The difficulty can be shown with the aid of a scaled model (Figure 2).

The central carbon atom of the heads of the amino acids, with the exception of glycine, are all assymetric, and happen to be of the l-variety. As a direct consequence of this, the nests of three OH groups on the alternate triazine rings are located above and below the plane of the fabric (see Figure 1), whereas the side chains are all above the plane. Half of the side chains are disposed "initially upwards," the other half "initially outwards" as shown in Dr. Wrinch's diagram (Figure 1) and correspondingly shown in Figure 2 by the match sticks (which represent the side chains).

The model is made on a scale of 10^8 to 1, or 1 cm.≡A°. The C–C internuclear distance is taken as 1.54, C–N as 1.47, C–H as 1.08, C–O as 1.43, and O–H as 0.97. The diameter of the hydrogen atom (more acceptably set at 2.13 or larger) is shaded down, for the sake of the argument, to 2.0; that is, the domain radius of the hydrogen atoms, beyond the nucleus, is made to be 1.0. This is in substantial accord with the value estimated (6) from the crystal lattices of methane and ethane,

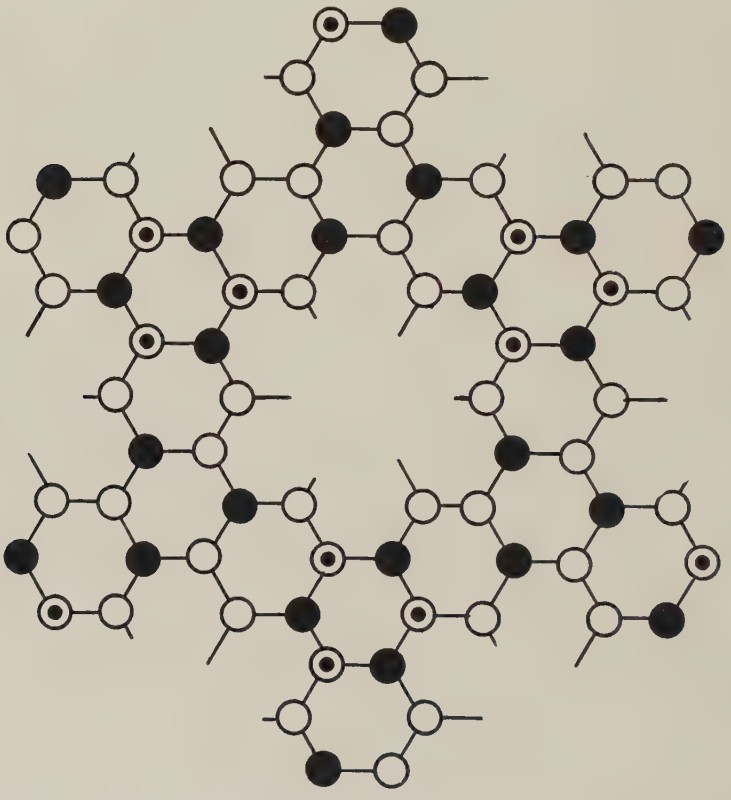


Fig. 1. A fragment of the cyclol fabric. Solid symbols represent nitrogen. Hollow symbols represent C(OH), hydroxyl upwards. Hollow symbols with dot in center represent C(OH), hydroxyl downwards. Hollow symbols with long arm represent CHR, direction of side chain initially outwards. Hollow symbols with short arm represent CHR, direction of side chain initially upwards.

and with the size needed to account for the cross-sectional areas of hydrocarbon chains in crystals and in oil films. The angle of the oxygen bonds is taken as 111°, the carbon bonds are tetrahedral, and I have allowed myself the license of making the angles of the three bonds of the nitrogen atom 109½°. (The angles are probably more like 108°). This license permits the assembly of the model as a "puckered" planar sheet, and amounts really to only a very small concession in the direc-

tion of conforming with Dr. Wrinch's practice. As a matter of fact, as far as the conclusion regarding the plausibility of the cyclol fabric is concerned, one can increase or decrease the bond angles by many degrees, without affecting the final clear cut conclusion.

One difficulty lies in the region of the fabric indicated by the white arrow in Figure 2. The three hydroxyl groups (shown here with oxygen atoms to scale) find sufficient room on the triazine rings for their accom-

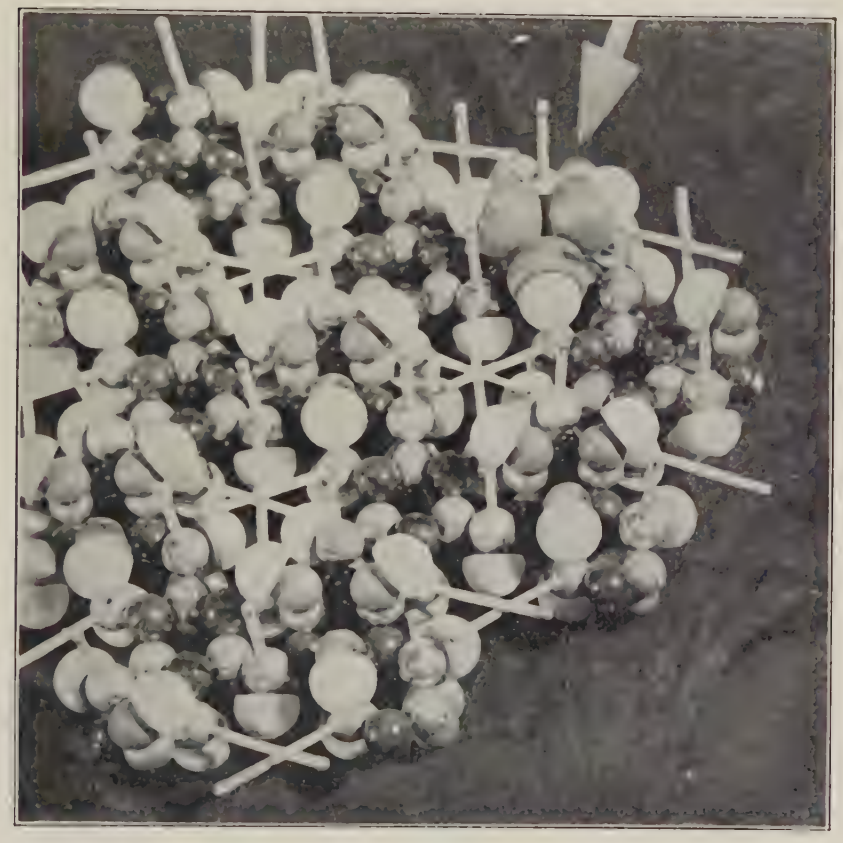


Fig. 2. View of model from above.

modation, either as formal OH groups, or with the H atoms resonating between pairs of O atoms. But the three "initially upward" side chains surrounding the rest of hydroxyls are very severely crowded for space.

A far more serious difficulty involves the "initially outward" side chains. Three of these extend into the central hexagonal cavity of Figure 1, and are shown as three crossed match sticks in the corresponding cavities of Figure 2. Now, it is to be borne in mind that these match sticks represent side chains which, on the model scale, are at least as bulky (with the exception of glycine) as normal hydrocarbon chains,

and in some of the amino acids they are as bulky as benzene rings (tyrosine and thyroxine, for example). It is obviously simply physically impossible to pack so much matter into so small a space.

Figure 3, which is Figure 1 reproduced more nearly to proper atomic scale, shows the difficulty clearly. HHH are the three hydrogen atoms which are carried by the same carbon atoms to which the three vertical ("initially upward") side chains, around the rim of the cavity, are also

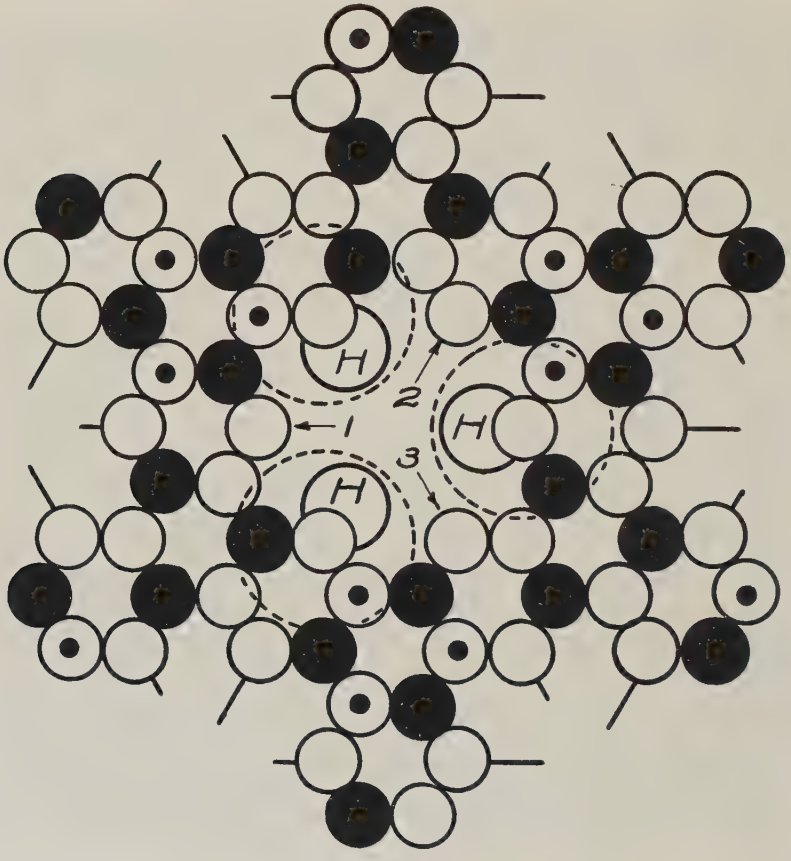


Fig. 3. Fragment of cyclol fabric drawn roughly to scale to show extremely small relative size of hexagonal cavity.

attached. The large dotted circles show the minimum space occupied by these vertical side chains of about 18 sq. A°. The points where the side chains "initially outwards" are supposedly attached are indicated by 1, 2, 3. The free space left in the hexagonal cavity, into which these three "initially outward" side chains are supposed to protrude, from their points of attachment to three carbon atoms bordering the cavity, and out of which they must extend and reach up (or down) to the surface in some way, is barely large enough to accommodate a single

extra hydrogen atom. Only if the three hydrogen atoms HHH were entirely removed *and* only if the three *vertically* placed side chains were entirely removed, would the free space of the cavity take care of a *single* normal hydrocarbon chain; and many of the amino acid side chains are larger in cross-section than a hydrocarbon chain, and furthermore *three* side chains are to be accommodated.

The protein fibroin is said to contain glycine to the extent of about 50% of its amino acid residues (1). It is conceivable that the Wrinch fabric could account satisfactorily for it and other possible proteins of at least 50% glycine content, *if* all of the glycine hydrogens were to occupy the "initially outward" positions, and *if* the "initially upward" side chains could also be attached to the fabric. The difficulty is that most proteins seem to contain much less than 50% glycine residues and many contain none at all.

Huggins (7) has already called attention to these space difficulties, as have also Neurath and Bull (8). Pauling and Niemann (9) have shown the improbability of the formation of the cyclol fabric on the grounds of energy considerations.

Hydrogen bond linkage of the diazine rings has been suggested (10), and more recently Dr. Wrinch (11) has described a modified fabric in which instead of a lactam-lactim there is a keto-enol transformation. But still the available space is far from adequate to permit the proposed disposition of the side chains. Huggins (12) has also made some further suggestions, which deserve consideration.

It is with regret that one feels compelled to abandon the cyclol fabric and its close cousins. Many of the attractive features of the cyclol fabric theory have been set forth by Langmuir (13). Dr. Wrinch's speculations have been immensely stimulating to those interested in protein structure, and it is still possible that her general picture of protein structure is not far from the truth. The objections raised here are directed against the specific cyclol fabrics which have been suggested.

On the other hand, we should not forget that a satisfactory accounting for the facts of protein behavior may very likely be rendered by a development and extension of the classical theory of long chain peptide structure; and as illustration of such an extension the recent fascinating and suggestive paper of Pauling (14) on "A Theory of the Structure and Process of Formation of Antibodies" may be cited.

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ECOLOGICAL FACTORS AND DROSOPHILA SPECIATION

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INTRODUCTION

In 1927 there appeared H. J. Muller's announcement of the artificial transmutation of the gene. This discovery was received with enthusiasm throughout the scientific world. Ever since the days of Darwin biological alchemists had tried in vain to induce those seemingly rare alterations in genes which were coming to be known as "the building stones of evolution." In the same year Charles Elton published a short book on animal ecology. It was received with little acclaim. That is not surprising. To the modern biologist ecology has seemed a bit out-moded, rather beneath the dignity of a laboratory scientist. Without detracting from the importance of Muller's discovery, in the light of the developments of the past 13 years we venture to say that Elton comes nearer to providing the key to the process of evolution than does radiation genetics.

Here is a quotation from Elton's chapter on ecology and evolution. "Many animals periodically undergo rapid increase with practically no checks at all. In fact the struggle for existence sometimes tends to disappear almost entirely. During the expansion in numbers from a minimum, almost every animal survives, or at any rate a very high proportion of them do so, and an immeasurably larger number survives than when the population remains constant. If therefore a heritable variation were to occur in the small nucleus of animals left at a minimum of numbers, it would spread very quickly and automatically, so that a very large porportion of numbers of individuals would possess it when the species had regained its normal numbers. In this way it would be possible for non-adaptive (indifferent) characters to spread in the population, and we should have a partial explanation of the puzzling facts about closely allied species, and of the existence of so many apparently non-adaptive characters in animals. . . . Finally what little we know about the regulation of numbers in animals enables us to say that the problem of the origin of species can only be successfully solved by the aid of work on numbers."

Two extreme views of the dynamics of evolution appear almost equally inadequate. Among paleontologists it has seemed popular to consider the evolving species as represented by one plastic individual projected indefinitely through time, molded into new form by the direct action of the surrounding environment. In contrast the theory of natural selection sets forth the premise that evolution is brought about by the action of selective factors on a population indefinitely large and in breeding equilibrium. Actually in any species there occur populations, finite in size, fluctuating possibly in rhythm with some climatic factor,

and also fluctuating arhythmically in size in response to variable arhythmic ecological factors and combinations thereof. In fact the general rule is irregularity and non-predictable variability. Thus the rise and fall of gene frequencies and the fixation or elimination of certain types are determined or conditioned by a set of variables that differ both in space and in time.

SPECIATION IN DROSOPHILA

To many biologists Drosophila means a small yellow fruit-fly, the species melanogaster. This, indeed, is the most famous of the lot, and used far more than any other for the investigation of genetic and cytological problems. However, the genus contains a great many other forms. From published descriptions and correspondence with collectors I have recently made out a list (certainly not complete) of 72 distinct types of Drosophila collected within the boundaries of the U. S. A. Over half of these we have had in culture in the laboratory at Wooster. Harrison Stalker and I have taken 26 species in Ohio.

One of the hoary arguments of the anti-evolutionist has been that never are new species seen to arise from old ones. By defining species as that group of individuals which can breed and produce fertile offspring the argument was properly sewed up in a neat scrap of fundamentalist logic. If, however, an array of cases can be presented within a group such as Drosophila, and shown to be seriated in regard to degrees of incompatibility between parental stocks and sterility of the hybrids, the case seems to be almost as strong for the occurrence of speciation as if one might sit quietly by and watch the whole business. And some study of the situation leads to the impression that probably the only reason we don't see the process is that we are too impatient to sit that long, or too undiscerning to see what is happening.

An examination of the genus indicates that not all species are equally dissimilar in morphological and physiological characters. Sturtevant (1939) has recently made a thorough study of the living species then available to him (over 40 in all) and on the basis of 27 characters for which each form was analyzed has proposed three sub-genera. Within these sub-genera sections are recognized. Thus the genus falls into groups of what appear to be more or less closely related species. At present immunological studies are projected or in progress in certain laboratories as a further check on these relationships. Although Drosophila of many species had been worked on much earlier, five years ago hybrid crosses had been secured only in the cases of simulans by melanogaster, pseudo-obscura A by B, and both races of pseudo-obscura by miranda. Two years ago in addition azteca had been crossed to athabasca, virilis virilis to virilis americana, and affinis affinis to affinis iroquois, seven cases in all. Today 20 cases of hybridization between diverse types are known in this genus.

Theoretically it would seem possible to seriate the differences or divergences between pairs of Drosophila types, so that it could be stated that these two were closely similar, a second pair more distinct, and a third even less alike, and so on. Actually in Drosophila an attempt may be made to seriate in terms of morphology, physiology and behavior,

sexual reactions, gonial chromosomes, salivary chromosomes, geographical distribution, etc. A man-made scheme would no doubt see to it that all fell neatly into the same order of seriation under the several criteria mentioned. Actually by no stretch of the investigator's best scientific imagination can this be done. A little reflection may lead to the conclusion that this is a normal state of affairs if the course of evolution is actually determined by a complex of interacting forces.

Following Dobzhansky's definition of species as that stage of the evolutionary process, "At which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding," we might attempt to arrange a series with regard to inter-type incompatibility and hybrid sterility. Difficulties in the way of applying the above definition of species and in seriation in this respect will appear presently. Not only do inter-group incompatibility and hybrid sterility, both factors in the physiological isolation called for by Dobzhansky's definition, frequently if not generally differ fundamentally in their causes and operation, but there is no uniform rule in regard to their relative strength in various cases. Further, there is sometimes great variation in the incompatibility of several strains of form A with one strain of form B, though all the strains of form A are highly compatible inter-se. Both incompatibility and hybrid sterility, but particularly the former, are highly susceptible to culture conditions. Darwin (1859) in his chapter on hybridism puts the case most clearly in these words, "It is certain on the one hand, that the sterility of various species when crossed is so different in degree and graduates away so insensibly, and, on the other hand, that the fertility of pure species is so easily affected by various circumstances, that for all practical purposes it is most difficult to say where perfect fertility ends and sterility begins. I think no better evidence of this can be required than that the two most experienced observers that ever lived, namely Kölreuter and Gärtner, arrived at diametrically opposite conclusions in regard to some of the very same forms. It is also most instructive to compare the evidence advanced by our best botanists on the question whether certain doubtful forms should be ranked as species or varieties, with the evidence from fertility adduced by different hybridizers, or by the same observer from experiments made during different years. It can thus be shown that neither sterility nor fertility affords any certain distinction between species and varieties." This quotation is given not because it is from Darwin, but because it states the case with a clarity to be looked for in vain in the writings of some modern students of this subject. Quantitative tables giving in per cents the sterility, incompatibility, or fecundity of first crosses and hybrids in Drosophila speciation studies have appeared and will continue to appear (the author is guilty of having perpetrated some of them; Spencer 1940a). They give a false impression of accuracy in the quantitative measurements of factors which are actually extremely susceptible to fluctuations in the environmental set-up and to hereditary variations difficult of analysis by which several strains of a given form may differ.

Through recent hybridization studies which have been reviewed elsewhere (Spencer, 1940b), it is becoming increasingly clear that this genus contains a vast array of recognizably distinct forms, some distantly and others closely related. However, as we seem to approach an analysis of the problems of phylogeny and to be in a position to arrange forms according to their natural affinities, disturbing questions arise. Which are the more nearly related, two stocks which have for a long time period been separated by some effectual isolating mechanism and yet which show little difference in morphology and physiology, or two forms which have more recently diverged but have undergone rapid changes in that part of the genotype which conditions morphological and physiological differences easily recognized? Are two forms living under conditions where the total metabolism of the species is low to be considered more closely related than two forms which live in the tropics even though both pairs have been effectively isolated for the same length of time? In fact the closer one approaches an analysis the less certain does an exact objective description appear possible. It would seem that the dynamic pattern of evolution projected through time could not possibly be accurately described in terms of the static pattern of evolution in space. Perhaps the sooner we realize that we are chasing a will-o'-the-wisp in attempting to arrange the forms of life in a static hierarchy of phylogenetic relationships the better. However, in the light of recent progress I should judge that we are on the verge of finding out much more about evolution than we have known. The taxonomist will continue to have an important, in many cases the most important, role to play in facilitating the study of groups of animal and plant organisms.

It appears that the changes which result in evolution are primarily changes which occur in the structure of the chromatin. A point which may still be considered debatable in some circles is that these changes are discrete and sudden at their primary level, though slow cumulative effects may accrue by gradual and progressive increase in the number of these inherited differences in two diverging stocks. It is unnecessary here to review the variety of processes, structures and characters in living organisms which may be changed by mutation. There is evidence that mutant factors may alter the whole pattern of events in connection with mitosis, may condition increased mutability at other loci, or may favor loss or addition of whole chromosomes. We shall not enter into the controversy as to whether so-called gene mutations are inherently different from small chromosome aberrations. Certainly, and what seems more important, mutation itself may produce slight or profound effects on an organism, may involve one or many so-called loci, may in short provide all sorts of changes which in turn may be combined to give an almost incomprehensible array of permutations. These may conceivably interact with the internal and external milieu in ways innumerable.

That characters by which hybridizing forms of Drosophila differ may be monogenic has already been observed. Pupa case color in Drosophila virilis virilis is gray and in virilis americana is red. A single genetic factor is involved. On the other hand it is not surprising that many of the inter-subspecific differences are multi-factorial. There is

no reason at present to believe that any of the characters morphological, physiological, or psychological by which two forms of Drosophila differ are determined by any inherently different mechanism than that which conditions those mutations with which the geneticist has been dealing for some years.

If this thesis be accepted it becomes possible to examine Drosophila populations for differences in gene and chromosomal structure and to consider such differences if found as the basic pattern for the first step in evolutionary divergence. If it be possible to find populations in which single gene or chromosome variants have become fixed it is valid to assume that the case is not inherently different from that in which an ensemble of genetic differences has accumulated and become fixed. We may go further and consider variations in frequency of unfixed genes in different populations to be an earlier and necessary step in evolution. It should be kept in mind that often the mutants with which we work may play a less important role in the development of new types than some which are less conspicuous but more fundamental in the sense that they may be acting to establish an isolating mechanism or to favor the group in natural selection when this becomes a directing factor.

ECOLOGY AND POPULATION MECHANICS IN DROSOPHILA HYDEI

Now, it is high time we get into the field. But being laboratory biologists suppose we shift over to field work by easy stages. Maybe we can learn something in the interim, and at least we can keep from getting our feet wet the first day. I want, therefore, to introduce you to *Drosophila hydei*. We shall go where this beast lives, watch it feed and breed, oviposit, overcome difficulties of temperature and moisture fluctuations. We shall see the eggs dry up one day, others hatch the next day. We shall see masses of semi-liquid medium shimmering in the noon-day sun with the writhing bodies of many thousands of tiny larvae. We shall see older larvae working down below the surface of medium now beginning to dry and later pupating in huge masses in still drier conditions. We shall see hydei die overnight by the tens of thousands, and leave a cold gray and lifeless world in a week or so where once there were literally a million insects breeding and feeding to the limit of the food store. We shall follow a few survivors through perilous days and weeks and months, and see them drop off one by one. We shall finally find the hardier ones and the luckier ones again breeding and see their grandchildren by the million; stark tragedy; the arrows of outrageous fortune; rare good luck; a perfect environment and for a time unlimited expansion with all the checks off; sizzling heat and stiffening cold; larvae drowned out and others dried up and still others coming through, surviving by strange coincidence a whole series of untoward events. This is everyday life for *Drosophila hydei* in any town in the northern part of our United States, and in any town worthy the name there hydei will be.

Drosophila hydei is a tropical species; there is some probability that it originated in Mexico. At least many closely related forms are to be found there. The species has worked northwards through the United States and is now well established in all parts of this country, but always

breeding in and about towns and dwelling houses unless temporarily carried out into the open country with garbage or other refuse. In northern latitudes each town forms a potential focus for an "island" population. Such populations pass through several overlapping generations a year with tremendous fluctuations in population size. Even in the mildest winters in this latitude hydei does not overwinter out of doors. The only survivors are those which find refuge in houses, fruit-cellars, restaurants and such places at the time of the first heavy winter freeze. I have followed the course of the hydei population in Wooster for some years. Every month of the winter this fly may be seen in certain restaurants; I have also known it to overwinter in cellars of private homes. It is a robust type, and can live in a dry room, sitting about on the walls for most of the time, provided every day or so it has access to food and moisture for a few minutes. Such an invironment is provided in restaurants; even though there is no opportunity for a winter brood of larvae the adults may carry through from autumn to spring. I have kept adults sufficiently long to be certain of this. In fact the overwintering population is generally in the adult stage. In general the size of a town or village will determine the chance of suitable places for overwintering and of these places being populated at the critical time in the autumn.

Among Drosophila species hydei is not a rapid breeder, the minimum cycle from egg-laying to newly emerged adult being 14 days. To this must be added a minimum of two days for maturing of the female and four days for maturing of the male after eclosion. Thus the life cycle is 18 days for males and 16 days for females under food and temperature conditions optimum for development. Actually the cycle under spring and summer conditions with the diurnal temperature rhythm is in the neighborhood of one month to six weeks.

At this season of the year (May), even though stores of food are available only a few scattered specimens of hydei will be found outdoors. By the middle of June to the first of July thriving colonies of hydei may be observed on garbage heaps, but still the maximum populations for available food are not present. Toward late August and early September the populations will often have built up to a maximum. However, July and August are likely to be hot and dry, and stores of food unless concentrated in large heaps may dry up before a generation of hydei comes through. In Ohio the months of September, October, and November generally see the peak populations of this species built up; particularly is this true during good fruit years, and with moderate autumn precipitation keeping food supply at the proper moisture content. With the heavy freezes generally occurring in late November and early December the hydei population rapidly falls off. Sometimes the species has bred up to such enormous numbers in town that it may be trapped in nearby woods. But this is due to population pressure and not because hydei is capable of establishing itself in natural woodland habitat.

Drosophila hydei is capable of withstanding extremely high temperatures in larval, pupal and adult stages. On a large citrus dump in southern California, containing tons of decaying oranges, grapefruit and lemons, and populated by an adult Drosophila population of many

millions, I made a study of temperature tolerance. It had been supposed that a temperature of 30° C., applied even for a few hours, would sterilize male Drosophila. On this citrus dump millions of adult *Drosophila hydei* were surviving with the air temperature a few inches above the surface registering 37° C. for several hours in the heat of the day. It was difficult to determine the exact temperature of the microenvironment forming the three or four millimeter film at the moist surface where the flies were gathered. A peculiar hovering reaction was noted under these conditions. Flies when disturbed flew with extreme rapidity but always in a dense swarm only a few inches above the moist medium and settled back on it quickly. At times the temperature of the medium in which larvae were burrowing was 36° and 37° C. Here many larvae were killed but others survived and when taken into the laboratory pupated normally; the flies emerging were normal and fertile. Thus larvae were observed in great numbers at temperatures at which well over half of them were killed; day after day the survivors had been subjected to these sublethal temperature shocks. I have kept hydei in adult, larval and pupal stages in a room above my garage in Wooster where mid-day temperatures went up to 36° C. *Drosophila hydei* may be the dominant form in summer populations in towns because of its ability to withstand intense heat. However, all species can stand higher temperatures than was formerly supposed. The lethal and sterilizing effects of high temperatures on Drosophila have been due not so much to the direct effect of the temperature as to the gases, particularly carbon dioxide, formed in poorly ventilated culture bottles.

Hydei larvae are also capable of withstanding drying up of food medium, at which time the larvae form small masses resulting in less surface loss of water. If then moist medium is again provided the larvae continue to develop although practically dormant during the drying period. The population pattern of *Drosophila hydei* brought about through the seasonal variations in temperature and moisture, with superimposed temporary and local fluctuations in food supply, moisture, competition with other forms, and temperature supplies the basis for the formation of local races or populations differing from others in the frequency of contained genes.

In a comprehensive series of papers on the mechanics of evolution in Mendelian populations Wright (1931; 1932; 1937) has presented a statistical analysis of the rate of evolution under various hypothetical conditions. For statistical purposes it has been necessary to reduce situations to their simplest terms, far simpler in fact then natural conditions warrant. Wright (1931) states briefly the role which fluctuating conditions may play in the following terms, "A question which requires consideration is the effect of alternation of conditions, large and small size of population, severe and low selection. The effects of changes in the conditions of selection have already been touched upon. Persistence of small numbers or of severe selection for such periods of time as to bring about extensive fixation of factors compromises evolution for a long time following, there being no escape from fixation except by mutation pressure. Many thousands of generations may be required after restoration to large size and not too severe selection, before evolu-

tionary plasticity is restored. Short time oscillations in population number or severity of selection, on the other hand, probably tend to speed up evolutionary change by causing minor changes in gene frequency."

It is possible to make a census of the genetic structure of Drosophila populations for a given year by taking a sample of the population and through inbreeding tests analyzing the genetic variability of the flies. The author (Spencer 1939) has attempted a fragmentary analysis of this sort for two widely separated *Drosophila hydei* populations, one living on a large citrus dump near Azusa, Southern California, and the other in the environs of Wooster, Ohio. The Azusa population is much the larger, perhaps at peak one hundred times the maximum Wooster population. The hot, dry summer at Azusa and the winter in Wooster constitute the critical reduction periods. The analysis has included the collection and examination of over 50,000 wild flies, and the rearing of over 5000 F_2 pair mating broods from some 1200 wild flies from the 1937, 1938, and 1939 Azusa populations, and from the 1937 and 1938 autumn Wooster populations. Inbreeding tests of 100 flies from Gatlinburg, Tennessee, have also been made. More than 180 cases of autosomal recessive mutants carried in wild flies have been found. In addition several sex-linked factors and autosomal dominants have been recorded.

The 1938 Wooster population was characterized by the high concentration of a small group of mutant genes, sex-linked vermilion in .48% of males collected, nicked wings in 4 out of 331 flies tested, gray body in 12 out of 500 flies, scarlet eye in 3 out of 500 flies, and rose eye in 3 out of 331 flies. The Azusa population showed no such high concentration of specific genes. On the other hand a significantly larger number of mutant loci per 100 flies tested were to be found from Azusa than from Wooster. Azusa, Gatlinburg, and Wooster populations have each given a different lot of mutant loci with little overlapping. The samples taken were inadequate to give an accurate quantitative picture of gene frequencies with the exception of vermilion; however, these qualitative results make it possible to plan experiments for adequate quantitative tests of yearly fluctuations in specific gene frequencies.

All over the United States there occur local populations of *Drosophila hydei*, varying in average size with the size of the towns and available food stores, undergoing periodic oscillations as well as arhythmic fluctuations due to ecological factors, and setting the stage for micro-evolution through rise and fall of gene frequencies. There seems little doubt but that here and there throughout this vast array of populations there occur cases of fixation of some mutant type. If this mutation should happen to initiate a partially isolating mechanism an insipient subspecies would be the result.

We have considered the case of *Drosophila hydei* in some detail because of the fact that its close association with man makes it possible to observe its activities more thoroughly the year round. These observations may serve in a way to bridge the gap between strictly laboratory and bona fide field work. We may think of a study of hydei populations as a large scale experiment carried on through the intervention of man but clarifying somewhat the problems to be encountered in studying species breeding in their natural range.

SOME ECOLOGICAL OBSERVATIONS ON OTHER DROSOPHILA SPECIES

If you have the time suppose we do some field collecting. It is the month of May. We go to the Providence mountains, a range in the Mojave desert of Southern California. We climb to the top of the ridge at mid-day. As the sun beats down on stunted pinon pine and bare rocks the temperature mounts well above 100° F. We pick up a club and break open a rotting specimen of *Echinocactus acanthodes*, the California barrel cactus. Inside is a great bowl of cactus soup, alive with Drosophila larvae. The adults sitting around on the inside of this bowl, little yellow fellows, turn out to be *mulleri mojavensis*, a subspecies which can cross with *mulleri mulleri* from Texas. Later we see as we drive along a desert road a belt of barrel cactus at elevations of around 3000 feet, a thin line of supplies but adequate to allow *mulleri mojavensis* to migrate all over the deserts from mountain range to mountain range. We go again up the arroyo, with not a drop of water in sight, in fact not a spring in the entire range. We set out traps in the late afternoon, and soon pseudo-obscura are flying in apparently from an environment as dry as tinder except for a little resin oozing from the pinons. Here and there is that spiny denizen of the desert, *Yucca mojavensis*. We kick over one of these tough plants and at the base find a mass of soft, moist fiber with mold growing in it. Where molds grow yeasts grow and there we find pupae which look suspiciously like those of pseudo-obscura.

We go some hundreds of miles away to Death Valley and drive up the desert floor of the valley during the afternoon. The thermometer registers 110° F. in the shade; but there is no shade. We camp for the night at Mesquite Springs; a clear cool spring running a quart or so of water a minute, a dozen screw-bean trees with gnarled and spreading branches, and plenty of fine soft sand. We hang our traps near the spring and with the aid of a flashlight visit them at night. Temperature readings show the thermometer creeping down toward 30° C., then lower and at around 27° C. the flies begin coming to the traps, first that yellow one we took in the Providence mountains, then a black, shiny one, then a stray pseudo-obscura or two. These last should be far away in the cool of the mountains at this time of year, but here they are. Perhaps they will live out the summer, more than likely not.

It is August and we are back in Ohio. We have set our traps in cool, wooded nooks along a branch of the Killbuck creek. We visit them in the early morning for even in Ohio it will be hot at midday and most of the Drosophila will have left the traps and found a cool spot at the warning of that rapid mid-morning temperature rise. At six or seven in the morning the flies are coming to the traps and we collect two or three thousand in a couple of hours. Back in the laboratory we check them over, the usual ones, perhaps 15 or 20 species. Here are a couple we ought to know, but they don't look quite right. We go to the species stocks and get out macrospina from Texas. The ones in our morning catch have the peculiar genitalia of macrospina but they are away off in eye color, body color and size. They turn out to be a new subspecies, breeding true to their peculiar character but crossing readily with Texas macrospina. We call them *macrospina ohioensis* (Spencer 1940b). Another morning we visit traps set in the swamps. This morning we go

early, four-thirty, and we get our feet wet. But we get something else as well. Two new Ohio species; but are they species? They are morphologically distinct with many character differences, but they will cross and their hybrid offspring are partially fertile. They cross with less ease than the macrospinas and we are not sure whether to call them species or subspecies. Somehow we can't seem to think that it makes much difference. On our trips we have taken flies that feed on fungus and others that feed on bleeding trees. We found larvae of the new swamp species feeding on rotting stocks of the arrow-weed.

We might discuss population patterns of flies breeding on leaf mold and humus all over our native woods, of flies confined to swamp habitats, of those which apparently feed mostly on fungus. There is much we do not know of the habits, the distribution, the ecology of these and others. We have a notion that field studies will help to answer some of the problems of speciation in the group. In any case it's a good excuse to be outdoors.

ENVIRONMENTAL FACTORS AND MUTATION

We have considered the action of the ecological pattern on distribution of mutant factors present in populations, resulting in shifts in gene frequencies; sometimes the elimination of mutant genes; at other times their rapid spread and even fixation. But there is more than a remote possibility that ecological factors may play an active role in producing the mutations involved. For many years men attempted to find the key to mutation. Muller finally found one key in X-rays. But he and Mott-Smith (1930) soon demonstrated that short wave radiation played no major role in natural mutation. Others, notably Jollos (1934), Goldschmidt (1929), and Plough and Ives (1935) have shown that sub-lethal heat shocks increase mutation rate. Gottschewski (1934) also demonstrated mutation increase through cold temperature shock. In recent years experiments have been reported, particularly by Russian workers, which indicated a sensible rise in mutation frequency following various other treatments, chiefly chemical. In fact we seem now to be in possession of too many keys. At the present time we may say that we cannot yet be sure that they all fit the lock.

Day after day, week after week, Drosophila in nature are receiving temperature shocks many of which are of the order of magnitude of those used by investigators reporting increase in mutation rate. The possible combinations of shock which might result from fluctuation in temperature, moisture and other ecological factors may conceivably be playing a direct role in determining the rate at which natural mutations are occurring. In fact experiments on wild stocks of *Drosophila melanogaster*, summarily reported in manuscripts received from Russian workers and read at the 7th International Genetics Congress in Edinburgh last summer set forth this point of view in some detail. This position may seem to be less satisfactory than the over-simplified view that some one definite factor could be discovered as the cause of mutation. The more we learn of the nature of the organic world the less chance there seems to be to reduce biology to a system of simple generalizations.

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Grain Pests

This authoritative book fulfills a definite need in economic entomology by bringing together all the information on a subject which heretofore has not been treated in this manner. It is written by one who has many years of experience in the experimental work conducted for the control of stored product pests.

The contents of the book is as follows, by chapters: The Insect Pests of Stored Grain and Milled Cereals; Controlling Stored Grain Insects on the Farm; Control of Insects in Grain Stored in Elevators and Warehouses; The Insect Problem in Flour Mills; Practical Control Methods in the Mill; Protecting Flour after Manufacture; Fumigants and Fumigation; The Common Fumigants; Flour Mill and Warehouse Fumigation; Fumigation in Atmospheric Vaults and Vacuum Chambers; Heat Sterilization in the Flour Mill.

At the end of each chapter is a selected list of references to the subject. An index completes the volume which is printed on heavy white paper by the offset process. The nature of the binding permits the book to remain flat when opened at any page.

It is an excellent contribution to economic entomology and will be a handy reference to the entomologist as well as the farmer, teacher and mill operator.

—*R. H. Davidson.*

Insect Pests of Stored Grain and Grain Products, by Richard T. Cotton. 242 pages. Minneapolis, Minnesota, Burgess Publishing Company, 1941. $3.00.

THE ORIGIN OF OHIO SOILS

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The soils of any region owe their character primarily to the conditions of environment under which they have developed. Just as in the biological world, also in rock weathering and in soil development, the key note is adaptation to environment. When rock material is exposed at the surface changes take place with the production of compounds which are more stable under that environment. Moreover, any change in environment will result in changes toward compounds which are more stable under the new conditions.

Factors of major importance in soil development include parent material, climate, vegetation, topography and drainage, and age. This is sometimes expressed in the form of an equation(1)[1]:

$$\text{Soil} = \gamma \text{ (climate, vegetation, relief, age, parent rock)}$$

If soil material stays in place for a sufficient time for the environment to be impressed on it, the result is expressed or shown in the development of layers or horizons differing in characteristics, such as color, texture, structure, consistency, etc., from the surface downward. This succession of horizons makes up the *soil profile.*

For information concerning soil material—parent material—we turn to our geologists. First, the bedrock of Ohio is everywhere sedimentary. West of a line drawn from Sandusky through Columbus the underlying rock is largely limestone, to the east sandstone and shale predominates. Actually much of the sandstone is in reality a siltstone—a very fine grained sandstone which weathers to silt.

Throughout about two-thirds of the state the surface materials are glacial in origin. The local character of the drift is shown in that 75 per cent or more is made up of material transported less than 25 miles. In western Ohio then, there is glacial limestone material, in northeastern and east central areas glacial sandstone and shale material. In northwestern Ohio and a narrow belt bordering Lake Erie in northeastern Ohio, the soil material is largely glacio-lacustrine in origin.

Beyond the glacial border in southern and southeastern Ohio the soil material is predominantly residual in origin. Its character depends on the nature of the local rocks—limestone and calcareous shale in Adams County in southern Ohio, and sandstone and shale in southeastern counties, except locally where limestone may be important; elsewhere red clay shale.

Climate is of first importance as an environmental factor in soil development. The most important climatic factors are rainfall and temperature, along with humidity and length of the frost free period.

[1]Numbers in parentheses refer to literature cited at end of paper.

Of special importance in soil development is the amount of water actually percolating through the soil. The actual soil climate will be conditioned by the slope of the land and the vegetative cover. The total rainfall, then is not an important factor, rather the effective moisture after losses by runoff and evaporation have been taken into account.

Transeau (2) in 1905 suggested the rainfall-evaporation ratio as an index to precipitation efficiency. Although records of evaporation were very limited, the concept was fundamental, and has been very helpful in evaluating climates. In 1935 Transeau stated that evaporation data was still very meager.

In the absence of data on evaporation, several attempts have been made to evaluate this factor from temperature records. Lang (3) in Germany in 1915 suggested the Rain Factor (annual precipitation in millimeters divided by mean annual temperature in degrees centigrade). The fundamental concept, that evaporation varies directly with mean annual temperature, does not agree with facts. Meyer (4), also in Germany, in 1926 used the N-S-Q value—the N-S quotient, that is precipitation in millimeters divided by the saturation deficit. The latter (S) was calculated from the vapor pressure for the mean annual temperature and the relative humidity. (V. P. $\times$ [100—relative humidity]).

Thornthwaite (5) has devised a new classification of climates, based on precipitation effectiveness and temperature efficiency. The sum of $\frac{P}{E}$ and $\frac{T}{H}$ ratios for each month gives a $\frac{P}{E}$ index and a $\frac{T}{E}$ index for the year. The value E is calculated from the temperature, by use of an equation derived from values for stations with evaporation data.

Based on any of these considerations, Ohio is in an intermediate climatic area, but not far from the borders of the cool humid area to the north, the warm humid area on the south and the prairie area on the west. Although there is not much variation in climate within the bounds of the state, it would not take much change in either temperatures or rainfall to shift the area into one of the other climatic belts. In fact, the vegetation shows relics of all three of the neighboring climatic belts. Some of the climatic relationships are summarized in Table I.

The vegetation factor will be discussed in detail by Dr. Transeau. Suffice to say here that most of our soils have developed under a dense mixed hardwood forest. The possible effects of past changes in climate and in vegation have not been evaluated.

In addition to the factors of climate, vegetation, drainage and relief in soil development, age is an important factor. Time alone is not the only factor, the rate of change must be considered. For the mature soil to develop the material must stay in place for a long period of time. But there are different degrees of maturity. For example, the soils derived from the Illinoian drift have leached to a depth of 8 to 10 feet, those from Lake Wisconsin drift to only 2 or 3 feet—this being a result of the difference in age. The drift of both areas is highly calcareous.

As a result of the action of these various forces on the soil material, profound changes have taken place, varying in intensity from the surface downward. The soil forming processes include the following:

1. The decomposition of the minerals of the soil material.
2. The accumulation of organic matter on the surface and within the upper soil horizons.
3. The leaching of soluble products of decomposition of both mineral and organic matter.
4. The translocation downward of soil material from some layers and the deposition in others.
5. The formation of new compounds by decomposition and by recombination.
6. The development of structure with the production of aggregates that break along rather definite lines.

TABLE I.

PRECIPITATION EFFICIENCY

	Ohio Gray-brown Podzolic Soils	Podzol Soils	Red and Yellow Soils	Prairie Soils
$\frac{P}{E}$ (Transeau)	80–100	130–150	100–130	60– 80
$\frac{R}{T}$ (Lang)	80– 90	110	65– 80	70– 90
N-S-Q (Meyer)	300–350	500–800	300–450	300–400
$\frac{P}{E}$ (Thornthwaite)	64–128	64–128	64–128	48– 64
$\frac{T}{E}$ (Thornthwaite)	48– 64	32– 48	64–128	32–128
Mean Annual Temp.	54°F. (12°C.)	40°F. (4°C.)	68°F. (20°C.)	42°F.–56°F.

In the investigation of soils their character, or morphology, is carefully studied in the field. Representative samples of the horizons are subjected to examination in the laboratory, their physical and chemical composition are studied. However, a chemical analysis must be supplemented by mineralogical studies to give an idea of the mineral composition of the material. A study of the mineral composition of the coarser fractions of the soil gives an idea of the unweathered, resistant minerals and is an aid in tracing the origin back to the parent material. Only within the last few years has it been possible to identify the products of weathering—the clay minerals (6). The methods for identification include the X-ray diffraction method, dehydration studies and others, along with chemical analysis of the clay minerals.

Studies have revealed the presence of a number of hydrated aluminous silicates. Only in tropical or subtropical regions does the silica-aluminium ratio approach the 2 to 1 value required for kaolinite—$Al_2O_3 . 2SiO_2 . 2H_2O$—the commonly suggested product of weathering of feldspars. Assuming a ratio in the unweathered mineral of 6 to 1 as in orthoclase—$K_2O . Al_2O_3 . 6SiO_2$—the common clay minerals in soils of humid temperate regions have a ratio of 3 or 5 to 1. These minerals have been identified as montmorillonite, beidellite, etc. They have high base exchange capacity, high water absorption capacity and high plasticity. Another group of minerals, variously called illite, glimmerton, X-mineral and hydrous mica, are somewhat similar to muscovite in composition, but contains less potash and more water by hydration along with silica and alumina.

In contrast to these are the clay minerals in lateritic soils of the subtropics in which the silica-alumina ratio is approximately 2 to 1 as in kaolinite. However, the common mineral has been identified as halloysite, which contains more water of hydration than kaolinite. They are characterized by low base exchange capacity and low plasticity. In laterite—a red soil of the tropics—the common mineral is a hydrated aluminum oxide. This whole field of the mineral character of clay minerals is a new one, the future should yield an abundance of important information.

Given sufficient time the net result of all of this is the development of a soil profile with layers or horizons with definite and distinctive characteristics. In case these processes go on unimpeded, either by erosion as on steep land, or by a high water table, as on very gently sloping or level land, the nature of the soil developed will be primarily an expression of the effects of climate and vegetation—external forces in soil development. These soils can be called mature soils or normal soils. Such soils, owing their characteristics primarily to climatic and biological (chiefly vegetation) agencies, occur in zones or areas corresponding closely with climatic and vegetation zones and hence, have been called *zonal* soils.

These are the naturally well drained soils of the state (7)—some are derived from materials high in lime, as in western Ohio, some from materials low in lime and some from noncalcareous materials as in northeastern Ohio. These are the best wheat soils of the State.

These features are characteristic of the great soil group, the gray-brown podzolic soils, and are distinct from the podzol soils to the north, the red and yellow soils of the south and the dark-colored prairie soils to the west. This soil zone extends from the prairie in Indiana and Illinois to the Atlantic seaboard. Throughout the whole area the main characteristics of the normal mature soil are essentially alike.

In association with the zonal (normal or mature soil) are soils which because of poor drainage, or steep topography have not developed the normal mature profile. These are called *intrazonal* soils, in that their chief characteristics are the result of some internal factor or condition. In one case adequate artificial drainage may be a first essential for their utilization; in the other case the erosion hazard may be a limiting factor.

In addition these soils are those which for one reason or another, show little or no profile development. Recent alluvial deposits are a good example. These are called *azonal* soils.

The typical zonal soil of Ohio, irrespective of soil material, has the following features:

1. A thin layer of leaf litter.
2. A dark grayish-brown layer, 2—3 inches thick.
3. A grayish-brown to brown soil.
4. A light yellowish-brown subsurface about the same in texture as the surface soil.
5. A yellowish-brown upper subsoil somewhat heavier than the surface soil, 10 to 15 inches thick, with a definite blocky structure.
6. The more or less unweathered soil material.

In association with the light-colored well-drained soils, and derived from similar soil material, are the poorly drained intrazonal soils. Those that are dark in color, with adequate artificial drainage prove to be the best corn soils of the state. The poorly drained light-colored soils, the gray soils, are characterized by a tight impervious subsoil. They are the most difficult to drain, the most acid, and are the lowest in productivity, of any of the soils in the association. To these gray poorly drained soils the group name of *planosols* has been given.

At the other extreme are the soils developed on steep slopes where geological erosion has kept pace with soil development. Here there is only a thin layer of soil over partially decomposed rock. Under such conditions the erosion hazard is the limiting factor in land use. Such soils are called *lithosols*.

Soils derived from similar soil materials, whose chief differences are the result of differences in topography and drainage are grouped in a *soil catena*, and the name of the best drained soil in the group is used for the name of the catena: For example, the Miami catena includes the soils derived from glacial limestone drift. The soils of a catena may be closely associated together in an area, on a farm, and even in one field.

As a result of the interaction of the forces of soil development, a variety of soils have been produced. Each has its distinctive characteristics. In its utilization in the production of crops useful to man each soil has its particular adaptations, its distinctive problems in soil conservation. Although the soils of the region naturally are of only moderate natural fertility, they are very responsive to good management and under the favorable climate form the basis of a stable agriculture.

On the level areas drainage is a problem. In the lake plain areas of northwestern Ohio, the heavy clay soils show a marked deterioration in structure with a resulting lowering in crop yields. In northeastern Ohio, the problem of soil acidity is uppermost. Better drainage on the smoother areas, erosion control on the rolling areas near the glacial border, are essential in an adequate land use program.

In southeastern Ohio the problem of erosion control is dominant in land use planning. Many steeply sloping areas, not adapted for rotation crops, can best be utilized for permanent pasture or for forests. The deeply leached soils of southwestern Ohio present a multiplicity of

problems. The extensive gray soils on the broad flats are difficult to drain, are highly acid, and are very low in productivity.

Thus each area with its distinctive soil association presents its special problem in soil utilization. Situated as we are on the eastern edge of the corn belt, and at the western border of the Appalachian Plateau, we have a variety of problems in soil conservation.

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Solids

Modern Theory of Solids by Frederick Seitz is the title of a new volume in the International Series in Physics. The work is an attempt by the author to present the subject matter so that students in physical sciences may obtain a certain knowledge of this branch of physics and for experimental men in the pure and applied fields of physics and chemistry, but at the same time also for men engaged in theoretical physics. For the benefit of the former groups certain tracts are marked with an asterisk to indicate that these are essentially mathematical in character and may be read only for their qualitative content. The theoretical man will often want to refer to and study these sections with some care.

The first four chapters are essentially introductory in character and present the subject matter in a classical manner. In Chapter Five the quantum theory is first introduced, part A being devoted to the postulates of the theory and part B to the interaction between matter and radiation. The next two chapters are in reality extensions of the theory to the many-bodied problem and application to problems in molecular binding. Succeeding chapters take up such topics as cohesive energy, work functions, electronic structure of metals, ionic crystals, valence crystals, semi-conductors and molecular crystals; the theory of conduction in solids and the magnetic and optical properties of solids.

In the opinion of the reviewer the volume is a valuable asset to anyone engaged in research in physical science. It is readable but at the same time a rigorous treatment of the subject is available to the reader who desires to look beneath the surface. It is well-illustrated throughout with clear and helpful diagrams. Modern Theory of Solids by Seitz is a valuable addition to the Internation Series in Physics.

—*H. H. Neilsen.*

Modern Theory of Solids, by Frederick Seitz. xv+698 pp. New York, The McGraw-Hill Book Co., 1940. $7.00.

PREHISTORIC FACTORS IN THE DEVELOPMENT OF THE VEGETATION OF OHIO

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During the half century that has elapsed since the organization of the Ohio Academy of Science numerous papers have been presented at its meetings in which the distribution of the flora and plant communities of Ohio was discussed. Most of these papers described local areas, county surveys, or the character of the successions in various parts of the state. Usually some attempt was made to relate the findings to climatic and soil factors. Others have discussed the relations of Ohio vegetation to that of surrounding states and have attempted to describe its origin.

During the past twenty-five years, the vegetation of numerous counties has been studied in some detail and checked with the survey records of pioneer days. At the same time our knowledge of the native flora of Ohio has been greatly increased through the finding of many unrecorded species and by the discovery of many new localities in which previously recorded species are living.

Meanwhile, additional details of preglacial, glacial, and postglacial changes in drainage in physiography and in soils have been brought to light by our geologists and pedologists.

The early authors who discussed the distribution of plants in Ohio were content to speak of the plants from the north and the south, or the east and the west. The publication of the glacial geologists, however, furnished a more intelligent basis for relating our present flora and vegetation to the climatic fluctuations of the past, especially the changes that resulted in the melting of the last ice sheet. This was followed by the northward migration of plants from south of the glacial boundary across the state to Canada. Certain authors talked of successive waves of tundra, boreal forest, and deciduous forest species moving northward into the lands uncovered by the ice. These generalizations definitely recognized the importance of (1) the historical factors as well as the complex of present day climatic and soil factors; and (2) distinguished clearly between the successions that are occurring under present conditions, and the successive vegetation types that may have occupied the state as a result of the larger prehistoric climatic shifts and physiographic changes (1, 2).

One of the members of this Academy also inaugurated in this country the now widespread study of peat deposits from the point of view of the kinds of pollen preserved in successive layers from the beginning of peat formation in ponds or lakes to the present time. These studies have given us by far the most definite records of the predominant vegetation types during prehistoric times (4). Most of the published records present the successive pollen frequencies of post-Wisconsin time, but it is not unlikely that in the course of time interglacial, and perhaps even preglacial peat deposits may yield similar information concerning

earlier migrations of vegetation during the Pleistocene and before. Fragments of this nature have been found, but apparently none covering very long periods.

From the pollen studies it now seems clear that during the post-Wisconsin epoch in central Ohio, forests of Jack pine, white spruce, and black spruce followed closely the retreating edge of the ice and that there was no distinct zone of tundra along the ice margin. White and black spruce forests were the predominant types for a very long time, perhaps the first half of post-Wisconsin time. This forest was at length invaded by northern oaks and pines. About the beginning of the last third of postglacial time, white pine with hemlock became the predominant species on the Ohio upland. Only during the last several thousand years have the oaks, hickories, and other deciduous species been dominant, following a rapid disappearance of the white pine and hemlock. The dominance of beech and maple over the greater portion of the state is the latest change in the prevailing vegetation.

At some time during the latter part of this record there was a long dry period that led to the invasion of Ohio by prairie species and communities similar to those of Illinois and Iowa. Whether it coincided with the dominance of white pine and hemlock or whether it resulted in the decline of this forest type remains to be determined (7).

The first effects of the Xeric period must have been the death by drought of trees in the swamp forests and the moderately moist habitats. This was followed by increased frequency and intensity of natural forest fires which opened up large areas of land to the prairie plant invaders. The prolonged droughts of the Xeric period also resulted in the elimination from the region of the prairie peninsula of many forest species which survived both north and south of this region.

The occurrence of many rare or out-of-range species on the peninsulas, lake shores, and islands of the upper Great Lakes is probably more related to their elimination elsewhere, especially from the area of the prairie peninsula by prolonged droughts in late post-Wisconsin time, than to the assumption that the areas in which they now occur were unglaciated. Most of these areas were not only glaciated, but were submerged in proglacial lakes for centuries following the slow retreat of the edge of the ice sheets.

At what time the upland hard pines and their associated shrubs and herbs came into Ohio from the Alleghany and Cumberland plateaus is unknown. Likewise, the time of the migration of sweet gum, pecan, pumpkin ash, and other species from the bottom lands of the Mississippi Embayment is not clear. It seems possible, however, that there were scattered upland pines here during the entire Pleistocene and that some of the Embayment species may have arrived in pre-Wisconsin time.

There are, however, some other isolated plant colonies in Ohio that seem to be definitely survivors of pre-Pleistocene time. They contain typically Appalachian species that may have come into the state by way of the pre-glacial Teays valley, or may at one time have been generally distributed throughout the Alleghany and Cumberland plateaus. At the present time, they are far separated from their next nearest stations in West Virginia and Kentucky and it is highly improb-

able that their occurrence here is accidental. As a rule they are hilltop and cove species.

We have called attention previously to the pre-glacial Teays valley which had its headwaters in West Virginia, Virginia, and western North Carolina. This great river system, together with other smaller rivers north and west, must be regarded not only as carriers of seeds and propagules to Ohio, but as agencies of erosion which carved a vast network of valleys and canyons across the mountains and plateaus. These valleys afforded not only a continuous series of bottom land habitats, but also parallel lines of steep slopes, cliffs, and ridge tops where the migration of upland species might readily proceed.

One of the striking facts about the species the distribution of which in Ohio may be directly or indirectly related to these river valleys and ridges is their absence at the lowest altitudes of the state. Among such isolated species are *Rhododendron maximum, Magnolia tripetala, Magnolia macrophylla, Styrax grandifolia, Pachystima canbyi, Calycanthus nanus, Azalea lutea, Oxydendrum arboreum, Chionanthus virginica, Polypodium polypodioides* and *Lygodium palmatum.*[1] The stations of these plants are singularly remote from other stations in the plateaus. Most isolated species are those which are characteristic of unoccupied or pioneer habitats, but most of these species are distinctly examples of undergrowth in well established forest communities.

Moreover, there are certain localities in the state such as Liberty township in Jackson County, and the Blackhand sandstone area of Hocking County (3) which have remarkable isolated assemblages of species growing in habitats that apparently are not unlike those in many other parts of unglaciated Ohio, but in which comparable assemblages are lacking. I use the term assemblages because the plants included are strikingly heterogeneous, as to habitat, taxonomic relations, and community affiliations. They range all the way from species of pioneer communities to those of climax associations and various ones are usually considered to be characteristic of boreal, hemlock-hardwood, deciduous, or prairie associations. Morevoer, the disjuncts include flowering plants, conifers, ferns, mosses, lichens, and algae. Both areas have a marked diversity of edaphic and microclimatic situations, but scarcely more so than various other areas in Southeastern Ohio. Both are areas having elevations considerably above the 900 foot level.

Assuming that our data are relatively complete, it is at least possible that the absence of these species in ravines, coves, and rock ledges remote from the higher uplands is a consequence of geological events connected with the earliest invasion of Central Ohio by an ice sheet, long antedating the Illinoian epoch. The northwestward flowing Teays river was dammed when the ice pushed across its valley and there must have resulted a rising flood that became a proglacial lake of vast proportions. Its southern and southwestern boundaries at the time of its maximum depth are not clear, but the lake probably extended as far west as the Licking valley of Kentucky, as far east as the present

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[1]Across the Ohio river from Lawrence and Scioto counties are isolated stations of *Pinus pungens* and *Quercus ilicifolia.*

Kanawha in West Virginia, as far north as Northern Ross and Athens Counties, and 40 to 50 miles south of the present day Ohio River.

Within the boundaries of this lake in Kentucky, which rose to levels above 900 feet, the geologists have discovered nearly a score of large glacial boulders. The composition of the rocks is reported to be unlike that of any rocks of the Ohio drainage basin, but similar to certain rocks of Eastern Ontario. These boulders must have been carried to their present location far beyond the Illinoian and Wisconsin terminal moraines, either directly in the ice of an earlier glacial invasion of Kentucky, or indirectly by icebergs floating on a deep proglacial lake. The evidence now available points to the latter alternative. Either alternative, however, would imply the formation of a large lake in southeastern Ohio, adjacent West Virginia, and Kentucky.

The duration of this lake is of the greatest significance as a destroyer of vegetation, since it existed a length of time sufficient for one to two hundred feet of silt and sand to accumulate. This silt eventually filled all the valleys to near the 900 foot level and obliterated the underlying topography. This conclusion is based on the fact that when an outlet was opened over a divide somewhere and the lake was gradually drained, many of the renewed streams did not return to their former valleys, but found new outlets to the Ohio River which was pieced together from various preglacial streams during the draining of this lake (5, 6).

A proglacial lake in this location must have been subject to great fluctuations in water level. To the north were the ice masses subject to rapid or slow melting, depending upon temperature and rainfall conditions. To the east and south the vast drainage area of the plateaus was subject to flooding through sudden melting of deep snows and heavy rainfall. The flood in the Ohio basin in the winter of 1937 caused the river to rise 60 to 80 feet in this same region. When the weather conditions at the edge of an ice sheet are compared with those of the present climate, and the fact that the outlets for the water were far more restricted than at the present time, it is not impossible to account for the large Kentucky boulder that was deposited at the 1000 foot level.

In speaking of the indirect effects of the ponding and reversal of drainage of this ancient lake, I have in mind the profound effect it had on the soils of the filled valleys, and the valley terraces. Thus, there was not only the destruction of all vegetation in the areas submerged, but a complete change in the soils to which plants that may have survived on islands and peninsulas might have subsequently migrated. When the stream flowed northwestward the soils of this area were derived from shales and sandstones of the plateaus. When the streams of the plateaus were ponded the streams from the glaciers carried calcium and magnesium carbonates from the limestone of central and northern Ohio. Moreover, it was not until the silts had been eroded and removed by subsequent streams that many of these habitats were uncovered and developed their present characteristics. Thus, today there are many localities in southern Ohio where, for example, rhododendron might be expected to occur, but in which it is absent.

It may at first thought seem difficult to believe that some of the rare plants in the Jackson and Hocking regions have been there during

the entire Pleistocene. Nevertheless, I am suggesting this possibility, and also that this earliest great proglacial lake[2] was one of the factors that contributed to the isolation of certain species in these remote localities. There may have been other and later factors that contributed to the extermination of these plants on other areas above the 900 foot level. One of my associates will in the near future publish further details concerning the possible boundaries of the lake and complete lists of the species in these two veritable living museum areas.

The impression is now growing that the historical factors are far more important in explaining the limits of associations and communities than we have ever imagined, and that vegetation patterns of the past remain for very long periods after the factors that initiated them have disappeared. In the list of papers below are other hypotheses concerning historic and prehistoric factors that may have influenced the present distribution of plants of Ohio. Also, there are other guesses as to how long some of the unusual habitats have been undisturbed, and when certain isolated groups of species migrated into Ohio. As more details of Pleistocene geography are discovered certain of these suggested explanations will be rendered either more plausible, more improbable, or definitely impossible and we shall be nearer a satisfactory history of Ohio vegetation.

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[2]This lake might very properly be called "Tight Lake" in honor of the geologist who first mapped the drainage modifications in southeastern Ohio.

More About Science in Relation to Society

The title of this book designates a topic almost as old as science itself and it has long been a favorite theme for lecturers and authors, particularly during periods of considerable social and political change. During our present turmoil, many individuals are expressing judgments on science (and almost every other subject also) and there is little agreement amongst them. We have before us a book in which the author offers information, almost entirely historical, to prepare individuals for doing their own thinking about the relationships between science and society; it is a presentation of data rather than of theory and for its purpose is worthy of earnest consideration.—*Carl Venard.*

The Social Relations of Science, by J. G. Crowther. xxxii+665 pages. New York, The Macmillan Co., 1941. $3.50.

THE AERIAL TRAVERSE

An Application of Aerial Photography to Geographic Studies

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Because of the comprehensive view of the landscape which it affords, the airplane makes possible a new mode of attack on geographical problems, especially on those which deal with any aspects of the distribution and special interrelations of geographic features. The observer in a plane is not limited as is the ground observer who depends on natural elevations for his outlook points. Whether the topography is flat or mountainous, altitudes may be chosen such that considerable areas can be included in a single view, and the point of view can be changed at will—a great advantage. The pattern of land utilization, the distribution of cultivated land with respect to topography, control of communication routes by topography, distribution of vegetation with respect to topography or to geological features, and numerous other aspects of geographical problems may be seen and studied in their mutual relations better from an airplane than in any other way. Photography preserves a permanent record of such information that can later be studied at leisure, and can be supplemented as necessary by work on the ground, provided the location of each of the pictures is definitely known.

The extensive network of airlines in the United States makes it possible for the geographer to select routes covering almost any of the principal types of geographic environment, so that in order to make extensive use of this new method of geographic study and recording it is generally not necessary to charter a special plane, although it may be desirable for special studies of particular areas.

LOCATION

As already suggested, for rigorous scientific work it is necessary that the exact, or nearly exact, location of each picture be known, so that the features which it shows can be properly placed on a map and so that the district may be visited later on the ground if necessary for proper interpretation of features shown on the photographs.

During flight, the procedure necessary for locating the pictures is to record the time when each picture is taken to the nearest practical division of a minute—generally to the nearest quarter minute—and also to record the time of the passage of the plane over or past objects such as towns, railroads, or rivers, which can be recognized on the small-scale map which the observer carries with him in the plane.

Such a map should be on a scale of about eight to twelve miles per inch. The writer has found the most satisfactory maps for this purpose

to be the State maps on those scales, which are available in almost any bookstore. Those maps commonly show cities and towns, railroads, and drainage—the features most readily recognized by an observer in a plane. Highways are not satisfactory because in most regions they are too numerous and are not readily identified. Consequently, automobile highway maps of the states are not satisfactory.

The approximate line of flight along a regular air route is, of course, known in advance. The observer marks in pencil a straight line along the proposed route which is helpful in enabling him to find quickly on the map objects over which he passes. It is also useful to prepare in advance on a 3 x 5 card a scale in minutes corresponding to the scale of the map used. For example, if the plane is flying at three miles per minute, which is perhaps a little faster than the ordinary cruising speed of the modern transports, the scale would show distances according to the scale of the map traversed in 1, 2, 3, 4, 5, and so forth, minutes. If one passes over clouds, or for any other reason loses contact with known ground features long enough to become doubtful of his location, the approximate location can then be determined quickly by applying to the map such a scale and measuring along the flight line from the last identified point.

The observer carries in the plane, in addition to the map and the scale just described, a convenient notebook in which to record the film roll number of each picture, a brief description sufficient to identify the subject, and the time the picture is taken. If pictures are taken in rapid succession, it may be possible to record only the time, but the picture itself will generally supply the needed information later.

With a little practice, the observer, knowing his approximate height (which can always be obtained from the pilot) learns to judge closely enough for location purposes the distance to objects on the ground, such as towns, bends in rivers, etc., so that it is not necessary to pass directly over them in order to use them for location.

PHOTOGRAPHY

In modern planes it is necessary that all photographs be taken through the plane window. The window, being made of laminated, shatter-proof glass, must of course introduce some distortion and blurring of the image, but so little that it is scarcely recognizable on the photographs. Disturbed air from the exhaust of the motor, which is sometimes in the line of vision for part of the photograph, causes more serious blurring, but even this is seldom recognizable. Even dirt on the windows, unless excessive, does not seem to cause difficulty. Satisfactory pictures have been obtained through the windows of a flying boat noticeably clouded with evaporated ocean spray. In photographing through a plane window, however, it is necessary that the camera be held as close to the glass as practicable without touching. To avoid the effects of vibration, neither the camera nor the operator's hands should be in rigid contact with the plane. If the camera is held too far from the glass, reflections of objects in the plane may cause trouble.

The Camera:

Any good camera may be used, but there are many advantages in using one of the "miniature" type cameras using 35 mm. film. One of the great advantages is that such cameras can be operated very quickly and easily, so that pictures may be taken in rapid succession, and another is that the number of the picture on the roll is shown on the exposure counter, so that each picture can be referred to by number. A third important advantage is that about 35 pictures may be taken before it is necessary to change rolls. With such a camera, enlargements to 5 x 7 inches have been secured that are microscopic in detail, that is, objects invisible to the naked eye on the enlargement can be seen with a hand lens.

Film:

To permit satisfactory enlargements, a fine-grained film is desirable. It is essential that the film have an emulsion yielding relatively high contrast. Ultra rapid film should be avoided because it tends to be flat and lacking in contrast, and to have coarse grain. A rapid emulsion speed is not necessary or desirable. Among Eastman films, Background-X (a commercial film prepared for the motion picture industry and not available in most photographic stores) has been found highly satisfactory. It is fine-grained, and has relatively strong contrast. Eastman Panatomic-X is satisfactory, but is not quite so contrasty as the Background-X. Dupont "Quarter speed" film has been used with success, but has perhaps a little too much contrast. Kodachrome can be used successfully, but color values may be slightly, though not seriously, distorted by the greenish tinge of the plane window.

Exposure:

The exposure should be such as will permit full development so as to obtain maximum contrast. The exposure will, of course, depend on the film used, and on light conditions. On an ordinary sunny day in the United States, using Background-X or Panatomic-X film and a light yellow (K-2) filter, a speed of f-6.3 and 1-100 second is perhaps average. The proper timing can best be obtained by testing the film from a high point of ground before the flight, recording light meter readings, making several exposures both longer and shorter than those called for by the light meter, checking the results after development, and choosing the factor which gives best results.

Unless the plane is flying close to the ground, its motion relative to the ground does not necessitate a rapid shutter speed. At heights of 2,000 feet or more, speeds as low as 1/40 or 1/30 second will give satisfactory results, although of course, if light conditions permit, shorter exposures are desirable. The principal cause of blurring is not the plane's speed relative to the ground, but motion of the plane if the air is rough. In smooth air, no trouble is encountered, but in rough air short exposures are necessary and even then it is difficult to avoid blurring. With a camera having a focal plane shutter, exposures less than 1/100 second can be used, but they give uneven lighting across

the film. Apparently there is an inertia lag in the shutter which results in one side of the film being exposed more than the other. A similar uneven exposure results when a picture is taken with the sun approximately either in front or behind the plane, because on the half of the picture toward the sun the haze or dust particles do not reflect light into the lens and consequently do not affect the illumination, but on the side away from the sun such reflection noticeably increases the light intensity. This effect, of course, depends on atmospheric haze, and is at a minimum on exceptionally clear days. It can be compensated by "dodging" during enlargement. On account of atmospheric haze, a filter is necessary for all pictures except those taken steeply down at relatively low altitudes. The writer has used the light yellow K-2 filter, but is not certain that this gives the best results under hazy conditions.

Development:

Development should be such as to give strong contrast and at the same time as fine grain as possible. Compared with ground photography, there should be a tendency toward under exposure and over development for the sake of contrast. The Eastman D-76 formula has given best results.

Stereoscopic pictures:

With a miniature camera permitting exposures in rapid succession, it is entirely practicable and for some types of work very advantageous to take oblique steresocopic pictures. The essential requirement is only that the two pictures composing the steresocopic pair be taken in as rapid succession as possible with the camera pointed at the same objects. For any geographic work in which it may be desirable to study relief features, stereoscopic pictures are especially useful.

LOCATING THE PICTURES ON THE MAP AFTER FLIGHT

Having obtained during flight the time when each picture was taken and the time when the plane passed over known objects or control points at intervals of 15 to 30 minutes, the procedure for locating the pictures on the map is to draw the flight lines as straight lines between control points on a base map of suitable scale, and then to obtain the location of each picture along these lines in porportion to time and distance. A slide-rule is extremely useful for this purpose. This procedure assumes uniform speed and straight line flight between control points. In a region for which detailed topographic maps are not available, locations so made must be accepted as final unless the observer at the time has made notes as to deviations from straight-line flight which may have occurred, or unless features shown on the pictures permit more definite location. Deviations from a straight course are rare, however, in ordinary scheduled flight, and locations so made will ordinarily be correct within a mile or two. Even in the rather featureless sand hills of western Oklahoma, the sites of pictures so located have been found without difficulty on the ground.

If a detailed topographic map is available, the location of the pictures can then be determined exactly because the locations on the smaller-scale map, made as above described, will be close enough so that on the detailed topographic map objects shown in the pictures can readily be found. It is then possible to make any necessary corrections in the line of flight and in the location of the pictures along it.

ADVANTAGES OF THE AERIAL TRAVERSE IN GEOGRAPHIC STUDY

By the methods above described it is possible by flight over a region on a clear day to make a photographic record of geographic features along the route with sufficient detail so that all significant changes in topography or culture may be recorded, as well as typical examples of each. The result is an essentially complete photographic record in traverse form. Such a record seems to have great possibilities for usefulness because the photographs tell the story much more vividly than it can be told in words.

EXAMPLES OF THE METHOD AS APPLIED TO OHIO AND THE PANHANDLE REGION OF TEXAS

The accompanying pictures are introduced to illustrate the types of geographical information obtainable by the methods described. The first eight pictures illustrate typical aspects of Ohio geography.

Figure 1 may be taken as representative of the Wisconsin glacial till plain. The ground is almost perfectly flat, drainage is as yet unorganized, and the soil shows the characteristic mottling of light and dark, in which the darker areas represent the black soil on the lower ground. Such glacial plains constitute the rich agricultural land of much of Ohio, Indiana, Illinois, Wisconsin, and Iowa. Interesting details in this picture are a trunk highway crossing the center of the picture; a field of wheat in shock lying beyond the highway at the left; and a field of uncut wheat that may be recognized on the near side of the highway at the right by the lines of oval dark spots which represent the positions where corn shocks stood the preceding autumn when the wheat was planted.

Figure 2 shows a typical aspect of the Illinoian glacial till plain about two miles northeast of Georgetown, Brown County, which appears at the upper right of the picture. Clearly this plain has been exposed to erosion much longer than the Wisconsin plain of Fig. 1 because stream drainage has here developed to an early mature stage. A well organized dendritic drainage system may be seen in the lower half of the picture, but in the upper half the original flatness of the till plain has not yet been destroyed. In the lower half of the picture the ravages of soil erosion can be clearly recognized in the white bands bordering each of the minor tributary valleys.

Figure 3 illustrates a typical floodplain—that of Scioto River immediately north of Piketon, Pike County (between Piketon and Waverly). The river, crossed by a bridge, appears in the foreground. In the upper right half of the picture is a large meander which has recently been cut off, and on either side of the floodplain the wooded

hills may be recognized. The picture is interesting primarily because it shows one of the commonest features of floodplains as they appear from the air, namely the "tracks," represented by curved bands of light soil, of ancient meanders showing successive periods of their growth and abandonment.

Figure 4 showing the floodplain of Scioto River immediately northwest of Portsmouth, Ohio, represents an even more striking development of floodplain features. Scioto River crosses the lower left and the Ohio the upper left corner of the picture. Many abandoned meanders can be seen, some of them still containing oxbow lakes, as at the upper left, and others made visible only by variations in the color of the soil. Some of these ancient meanders and former ox-bow lakes, though plainly visible, are so nearly obliterated topographically that, as shown near the center of the picture, the farmers plough across them without deviation. The border of the floodplain is followed by a highway, beyond which are the wooded hills. A suburb of Portsmouth (Bertha) appears at the right center.

Figure 5 shows an interesting development of orcharding on the floodplain and low terrace on the Ohio side of the Ohio River, about seven miles east-northeast of Huntington, West Virginia. The bluffs bordering the terrace appear at the lower right. Extensive orchards may be readily recognized by their distinctive pattern. Soil differences resulting from meander growth of the Ohio may be detected by color changes and seem to have been reflected in property ownership, as indicated by the pattern of the fields.

Figure 6 portrays a typical example of the unglaciated portion of eastern Ohio. Erosion of the region, whose relief is about 300 feet, has passed somewhat beyond maturity. Cleared farmlands are divided almost equally between upland divides and valley bottoms. About one-third of the area is wooded—mainly on the steeper valley sides.

Figure 7. In the maturely dissected, unglaciated Alleghany plateau, soil erosion is serious. One of the most effective means of combatting erosion is "strip cropping," of which a particularly fine example is here shown. Strips of ground contouring the hills are planted with different crops in such a way that a crop, such as corn, that promotes erosion alternates with another like alfalfa, that holds the soil in place.

In the center of the picture the corn shocks on three of the strips are readily recognized. The darker strips are probably grass or alfalfa, and the lighter probably wheat.

Strip cropping is not yet extensively used in the plateau, but a few fields so cultivated may be seen in almost every neighborhood (see Fig. 6 near center) and soil conservation agencies are urging its wider adoption.

Figure 8. A type of mining that is extensively developed in eastern Ohio—the strip mining of coal—is strikingly revealed from the air.

In strip mining, which requires that the coal bed lie close to the surface over considerable areas, the overburden of soil or rock is removed by power shovels which strip it from above the coal and swing it to one side where it is piled in great wind-rows, such as are shown on the photograph. In this area an overburden of nearly 50 feet has been

removed to recover a bed of coal 30 inches thick. The aftermath of strip mining, as is well illustrated on the picture, is almost complete devastation of the area mined. Rehabilitation of the land ruined by strip mining is one of the problems confronting the State. For agriculture, the land is probably permanently ruined, but certain types of forestry offer possibilities for rehabilitation.

By way of contrast to Ohio, two photographs are introduced illustrating a totally different geographical environment—the Panhandle region of Texas.

Figure 9 illustrates the sand hills which border the Canadian River, a short distance north of the village of Clear Creek, Hemphill County, Texas. A railroad crossing the lower right corner of the picture serves as scale. Sand has been blown for several miles to the east, from the usually nearly dry bed of Canadian River and piled into low, irregular dunes, such as those shown on the photograph. Most of this sand appears now to be stationary, as is evidenced by its partial vegetation cover, and only occasionally do active "blow-outs" testify to present movement of the sand. This condition suggests a more arid climate at the time these sand hills were formed.

Figure 10, taken late in the afternoon along Red Deer Creek, about five miles northwest of Miami, Roberts County, Texas, is a beautiful study of erosion working headward from one of the larger streams into the grassy plains of the Texas Panhandle. Scale is indicated by a railroad which crosses the picture beyond the sandy bed of the "river."

Fig. 1 (upper). Till plain of the Wisconsin glaciation, with characteristic soil mottling. Looking north. Center of picture 39° 47.5′ N., 83° 13.6′ W., 12½ miles west of Columbus, Ohio.

Fig. 2 (lower). Till plain of Illinoian glaciation northeast of Georgetown, Ohio. Center—38° 52.6′ N., 83° 52.7′ W. Looking southwest.

Fig. 3 (upper). Floodplain of Scioto River south of Waverly, Ohio. Looking north. Center—39° 5.5′ N., 83° 00.5′ W.

Fig. 4 (lower). Floodplain of Scioto River near its junction with Ohio River. Looking south. Center—38° 44.9′ N., 83° 1.0′ W.

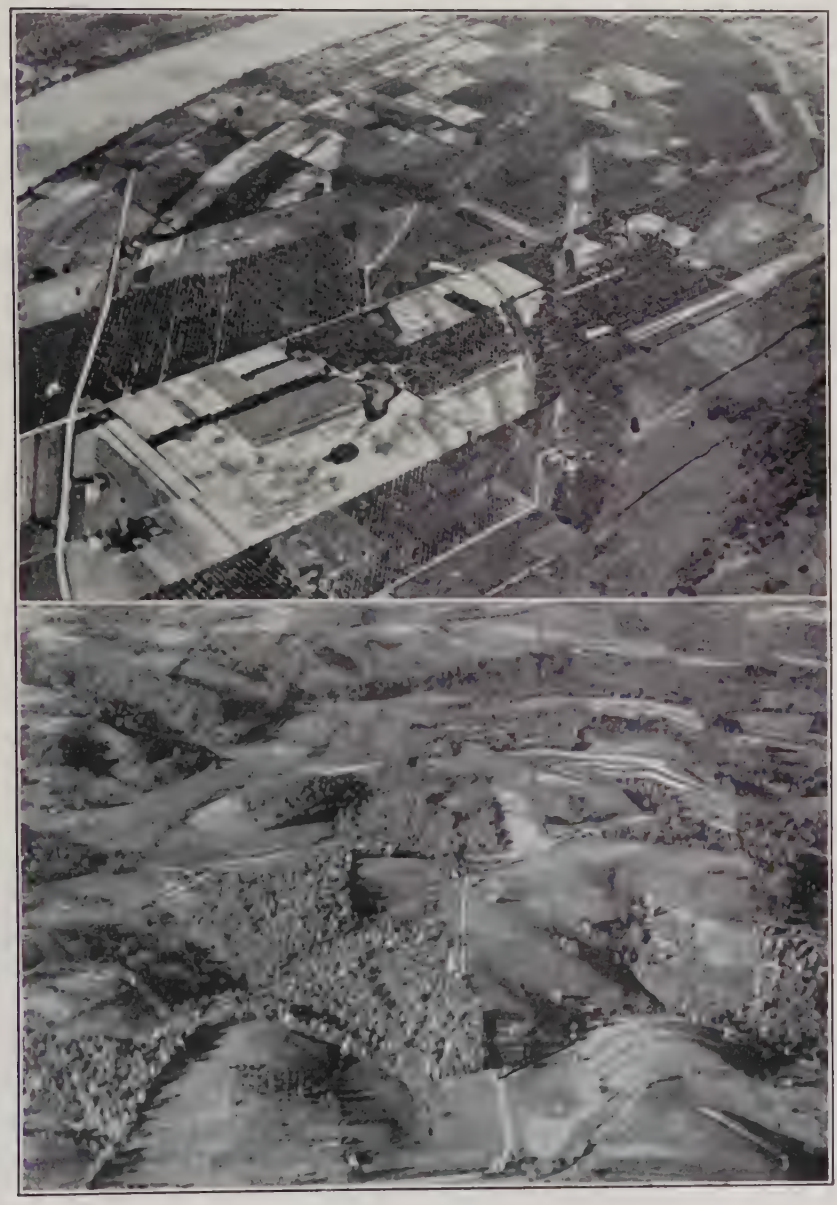

Fig. 5 (upper). Orcharding on floodplain and terrace of Ohio River about 7 miles east-northeast of Huntington, W. Va. Looking southwesterly. Center—38° 27.5′ N., 81° 20.5′ W.

Fig. 6 (lower). Typical unglaciated plateau of eastern Ohio 1¼ miles southwest of Freeport, Harrison County. Looking north. Center—40° 2.5′ N., 81° 17.1′ W.

Fig. 7. Strip cropping to control soil erosion on the unglaciated Allegheny plateau. Looking north about 3 miles northwest of Avella, Pa., about one mile east of the West Virginia line. Center—40° 18′ N., 80° 30′ W.

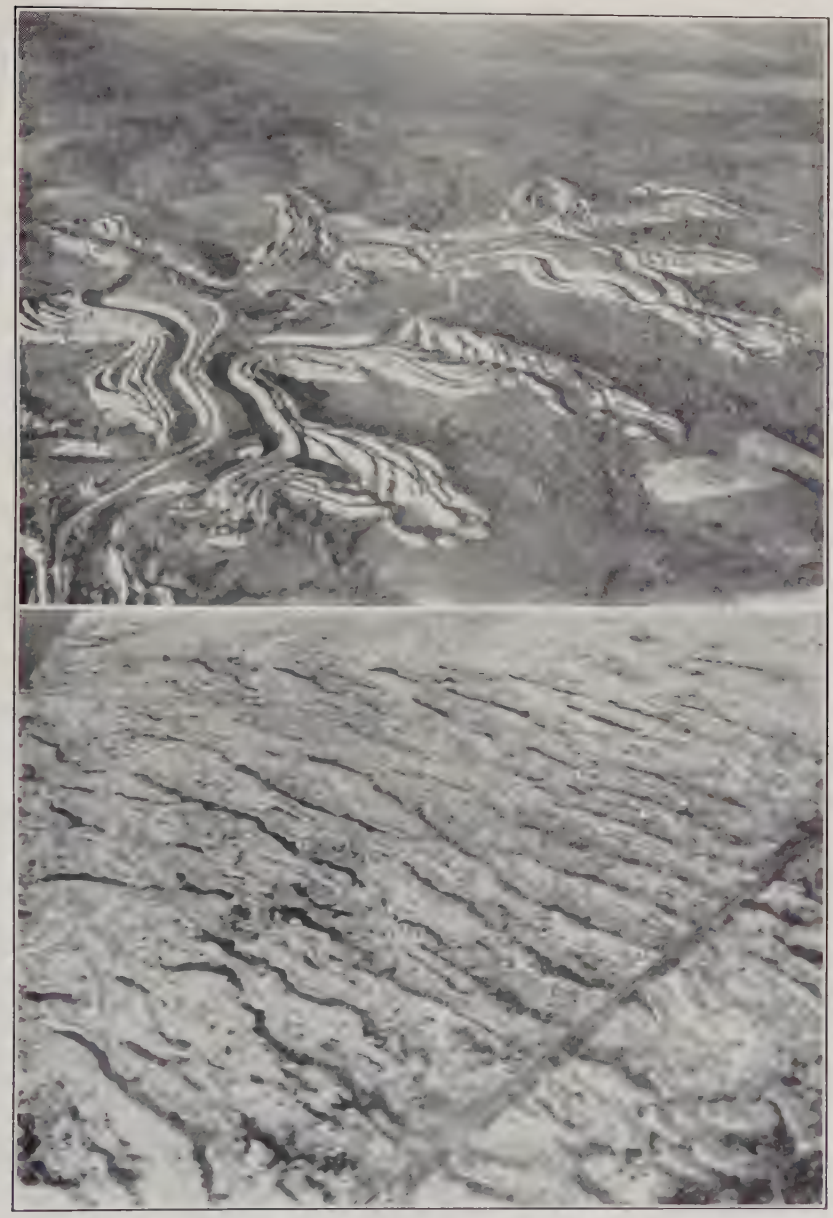

Fig. 8 (upper). Strip mining for coal in eastern Ohio. Looking northeast at large mine four miles south of Dresden, Muskingum County. Center—40° 4.1′ N., 82° 2′ W.

Fig. 9 (lower). Sand hills along east side of Canadian River north of Clear Creek, Hemphill Co., Texas. Looking northerly from 35° 57′ N., 100° 15.3′ W.

Fig. 10. Study in erosion along Red Deer Creek, Roberts County, Texas, about five miles northwest of Miami. Looking southerly from 35° 43′ N., 100° 43′ W.

POSTGLACIAL VEGETATION IN THE ERIE-OHIO AREA

PAUL B. SEARS
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It is fitting that the Golden Anniversary program of this Academy should devote some time to the problems of Ohio vegetation. The diversity of natural vegetation in Ohio has interested observers from the days of the first explorations down to the present. Before the founding of the Academy, surveyors, geologists, and botanists all contributed to the record. A notable instance was Dr. John L. Riddell (1) who saw in the prairies of Ohio a remarkable phenomenon.

In more recent years the Academy itself has generously encouraged studies of Ohio vegetation. Needless to say the pattern of this vegetation has had profound influence on the agricultural and industrial life of the state. During the past twenty years, beside the important work of Dr. Braun at Cincinnati (2), there have been numerous studies by Dr. Transeau and his associates at Columbus. These studies have had valuable results in their application to pest control (3). They have illuminated the work of a generation of young biologists who are now applying their knowledge to problems of land use and management throughout this and other states. I am glad to record such a debt to the Academy and the many colleagues who have labored in its ranks.

Some notion of the diversity of Ohio vegetation may be obtained from Figure 1, showing various types and their irregular pattern of distribution. It may be said at once that no simple factor can be adduced as an explanation. No map of climatic configuration that I have ever seen can be superposed on this map of original vegetation. One can, it is true, see evidence for some large physiographic influences, notably glaciation and lake retreat (4). Yet detailed profiles through various types of plant community certainly show that here again there is no simple relationship between topography and vegetation.

One needs no better evidence of the multiplicity of factors operative in the Ohio landscape than to see how comfortably—until the axe and plow destroyed them—species and communities of differing geographical and climatic affinities got on in close proximity.

Transeau's paper on the Prairie Peninsula (5) in addition to its clear formulation of numerous problems, has served to emphasize the relative and complex character of Ohio climate. As time goes on we shall learn much more about this matter from the studies now under way in the Muskingum watershed (6).

Author's Note: Since preparing the accompanying article, the writer has made an extended study of the literature dealing with the question of xerothermic postglacial climate. In view of recent evidences from Europe, the references in this paper to a xerothermic period ought not to be regarded as excluding the possibility of significant aridity earlier than the pine period here referred to. However, it should be stated that no American bogs thus far examined give any indication of such conditions.

At the other edge of the prairie, Weaver and Albertson (7) have shown how definite may be the effect on community composition of a few years of protracted drouth. And I may add that my own casual examination of tree rings in the Osage region indicates that recurring drouths, lasting from two to ten years, have characterized at least the past two hundred years.

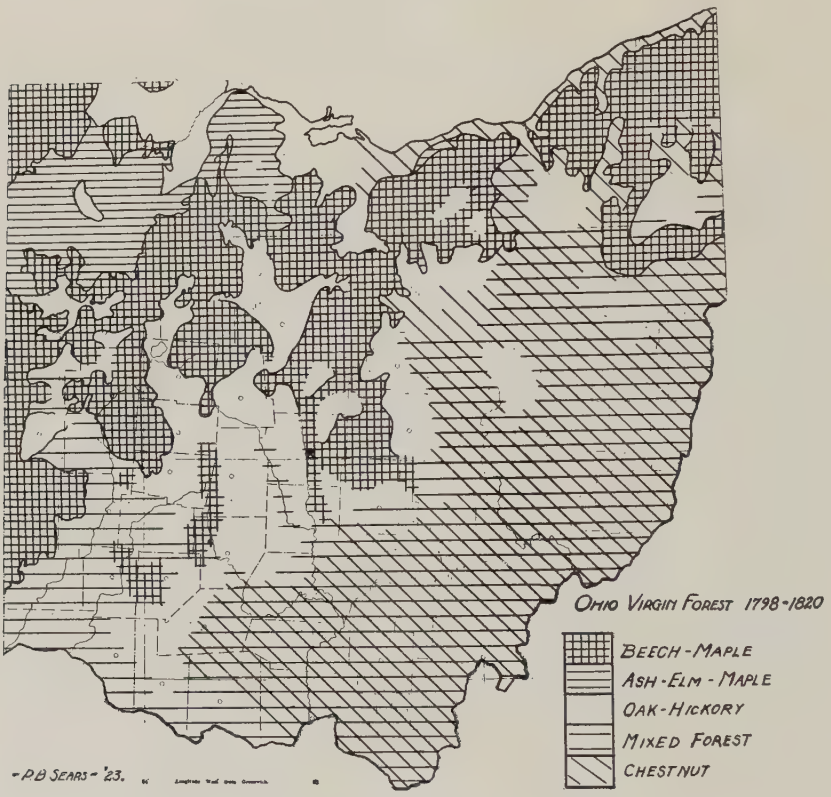

Fig. 1. A map of the original vegetation of Ohio based upon records of early surveys.

Because of the inadequacy of explanation based on existing conditions, students of vegetation have followed the steps of Asa Gray and other taxonomists in searching for historical data. In the case of Ohio, two important types of community—bog and grassland—present in a deciduous forest region have for many years emphasized the need for and importance of historical study.

Beginning in 1925 and for ten years thereafter, I employed the technique of pollen analysis in trying to trace the general course of vegetation changes throughout the Middle West. Several years were required for getting acquainted with the American pollen (8), a circumstance which materially slowed the procedure.

Taxonomists and others had already accumulated a good deal of evidence, not only of migration in the wake of the retreating glacier but of postglacial changes which involved east-and-west shifts of vegetation (9), presumably due to changing humidity of climate. The former presence of coniferous forests in Ohio and elsewhere in the deciduous forest region was readily established by pollen analysis. Its demonstration is now a routine experience which can be used as a laboratory exercise. Wherever there is a peat deposit whose sedimentation began in late glacial time, the presence of abundant coniferous pollen can be shown by microscopic examination of the deep layers of peat or marl.

It happens that the first bog I studied was likewise the oldest, situated on the crestline of the state, east of Bucyrus (10) (Fig. 2). The record here begins with an abundance of fir, gradually shifting to spruce,

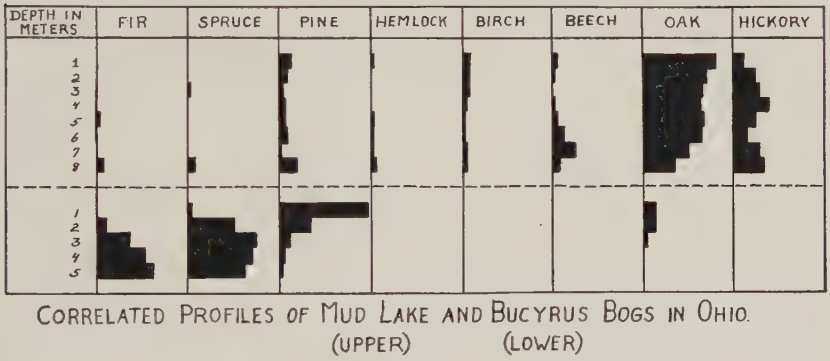

Fig. 2. Combined pollen profile of Bucyrus (lower) and Mud Lake (upper) bogs.

and then to pine. The pine in turn is replaced by increasing amounts of hardwood pollen, but the record is not complete because the top of the deposit has been destroyed.

This pine maximum toward the end of coniferous time is widespread, and was interpreted, correctly, I still believe, to indicate a period of increasing aridity.

Subsequent analyses of bogs in deep kettle-holes, where peat formation has gone on more or less continuously up to the present, indicated that the deciduous period has been much more prolonged than we were to suspect from the truncated record of the Bucyrus bog. One of the best examples of this is the Mud Lake Bog in Ashland County (11). Among our unpublished records of some 25 bogs, however, we have found ample confirmation. This is also generally true of profiles that have been published by the growing number of other workers throughout Eastern North America.

Taking the Mud Lake Bog as an example (Fig. 2), we find a strong showing of beech and hemlock at the beginning of deciduous time, then once again in recent layers, a behaviour paralleled by the record of birch.

Hickory, however, shows a reciprocal curve, being strongest about two-thirds up from the bottom, when beech and hemlock were greatly reduced.

Here again we reasoned that the beech and hemlock, replacing pine, indicated warming and increased moisture. Above that point the hickory maximum we interpreted as a second dry—but now warm—interval whose waning was marked by the return of beech and hemlock. If our reasoning was correct, we had established the existence and position of the elusive xerothermic period postulated by Gleason (9) and others as an explanation of the prairie relicts east of the present prairie.

Let me acknowledge that this was dangerous reasoning, based on a minimum of evidence. In justification let me say that the profiles, instead of being erratic, showed long consistent drifts in the course of change, and that the genera we were using are excellent climatic indicators. It is of interest that Professor Fuller at Chicago, on first seeing it, pronounced the sequence obtained from the two bogs—Bucyrus and Mud Lake—an excellent confirmation of the Blytt-Sernander hypothesis of postglacial climate that had been developed in Europe (12).

Two problems immediately presented themselves. One was that of confirming or disproving the general sequence. The second was that of chronology. The first problem required the widescale study of peat profiles and their comparison. This had to be done as rapidly as good work would permit, and to that end a considerable number of other workers were given assistance in learning the proper technique.

It is of course clear that no analysis is complete without supplementary study of the basin from which the peat comes. But the basins will keep, and the peat frequently in these days of rapid exploitation will keep, and the peat in these days of rapid exploitation frequently will not. For that reason, our first objective was to secure just as many pollen profiles as possible.

The results of these studies showed clearly enough that there are definite regional types of peat profile, with their characteristic pollen trends. Furthermore, the presence of an early dry—cool—pine period seemed to be pretty general in the older, longer profiles. Above that, corresponding to the Mud Lake hickory maximum, presumably warm-dry, many at least of the profiles showed a maximum of oak as compared with more mesophytic species. The most important exception seemed to be the findings of Voss in Lake County, Illinois, to which further reference will be made.

As to the problem of dating, we did as others have had to do: used what means we could, pending the time when an accurate varve chronology would be afforded to us. So we obtained by three independent means some notion of the normal rate of peat accumulation. Knowing full well that this sort of measure has to be used with the utmost caution, we at least obtained estimates which indicated that we were dealing with magnitudes of the same general order as the precisely dated European records (13).

Meanwhile criticism arose from several sources. Doubt was expressed concerning the dependability of our counts, based on 100 to 200 grains per sample. As a result, Barkley (14), working in Oklahoma, made a

study of the statistical principles involved and showed clearly that no practical gain may be expected by counting more than 150 grains per sample.

The second criticism was based on the studies of Voss (15) in Illinois, already referred to. It has been urged by Fuller (16) so that some attention should be given to it here. The Lake County profiles of Voss showed a replacement of conifers by deciduous forests, mainly oak, at the end of the first third of the record. Thereafter the deciduous forms exhibited what seemed to be an irregular fluctuation, giving no clear evidence of any climatic or vegetational change.

It should be noted, however, that Voss' own profiles from farther north showed a concave conifer curve, increasing at the top, complementary to a convex deciduous curve. This would appear to agree in general with either (a) the upper portion of our Ohio curves, or (b) with our whole curve if we assumed that the humid beech-hemlock interval was merely a local phenomenon.

To allow for this possibility, and to afford a scheme that could be definitely tested, I then proposed an hypothesis that postglacial time had been marked by a long period of warming and perhaps drying, up to a maximum from which it has since receded (17).

This of course does not take care of the Lake County bogs. But in explanation it must be said that there is no means of distinguishing the species of oak in these profiles from Illinois. And anyone who knows the oak-hickory region is well aware that red oak is more mesophytic than certain members of the white oak group. A fluctuation from red oak to white oak or vice versa in this region would be very significant if we could demonstrate it. But with all species of oak necessarily lumped, any such phenomenon would remain masked.

Furthermore, these profiles contain no mention of grass pollen, although it usually is pretty well preserved and should be of the greatest importance in indicating fluctuations at the margin of the grasslands. So far as climatic evidence is concerned, then, my own judgment with regard to the Illinois bogs is to recognize that they fail to support the xerothermic idea. What they might reveal if the species of oak could be determined and if grass pollen could be found in them would be of great interest and value.

Meanwhile, serious considerations were brought forward by the thorough studies of Wilson in Northwestern Wisconsin (18), where pollen profiles had been studied with reference to the recessional stages of Lake Superior and the present-day plant successions. In general the profiles fitted into the series obtained by workers from Minnesota eastward through Quebec. Predominantly coniferous at the base, they exhibited a slight shift toward oak at higher levels, followed by a recent increase in spruce, i. e., a return of conifers. Yet when compared with current successional changes these profiles in Wisconsin seemed explicable in terms of local plant succession under a climate like the present.

Without some basic climatic change, however, one would scarcely expect to find such a remarkable parallel trend in local succession on a front extending from the northern Great Lakes to the Atlantic. More-

over, both in Europe and America the sequence, conifer-hardwood-conifer, has been established as characteristic of interglacial periods, one of which the present may well represent.

It is of the greatest interest, therefore, to know that a recent study[1] of Ohio peat deposits has enabled Wilson to correlate them with the Wisconsin profiles and confirm the fact of recent climatic change, including a xerothermic period corresponding to the oak maximum noted by him.

Meanwhile it is in order to present the results of further study at Oklahoma, Oberlin, and Yale. Miss Eleanor Galloway who had been trained with Dr. Wilson was given access to much of my unpublished material and found a definite relation between profile type and bog

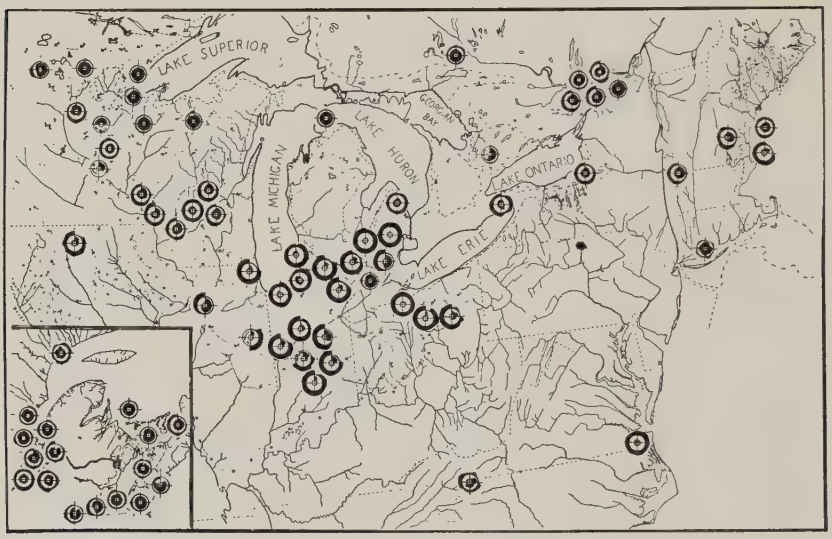

Fig. 3. Clock diagrams showing postglacial changes in frequency of conifers (inner circle) and deciduous (outer circle) trees. (From Preston Smith.)

location. Her manuscript is not now at hand, but as I recall it, a line approximating the Fourth Wisconsin Substage limit is roughly a boundary south of which are bogs whose profiles are mainly deciduous, while those to the north are largely coniferous. Mixed types are intermediate in position.

Last year this problem of correlation was resumed by Mr. Preston Smith at Oberlin, our immediate aim being to trace the course of post-glacial migration of certain trees. First compiling a critical map of glacial boundaries, data from nearly 70 bogs were assembled and plotted in the form of clock diagrams. Proceeding clockwise, these circles show the changing frequency from bottom to top of the bog.

The first of these shows the relative position and abundance in each

[1]Unpublished. Not seen until after this paper was read before the Academy.

profile of conifers (inner) and deciduous (outer) species (Fig. 3). The second gives the same information for hemlock (inner) and beech (outer) (Fig. 4). No correction is made for differences in time represented by a given profile, except as this is indicated by the position of each bog.

Yet the map shows very clearly the location of Miss Galloway's deciduous, mixed, and coniferous profile types with reference to glacial retreat. Likewise the southwesterly movement of *Tsuga* and the northerly movement of *Fagus* are evident.

Further light on postglacial migration is available by taking five representative genera, *Tsuga*, *Quercus*, *Fagus*, *Carya*, and *Tilia*, and noting the order of their appearance in as many profiles as possible.

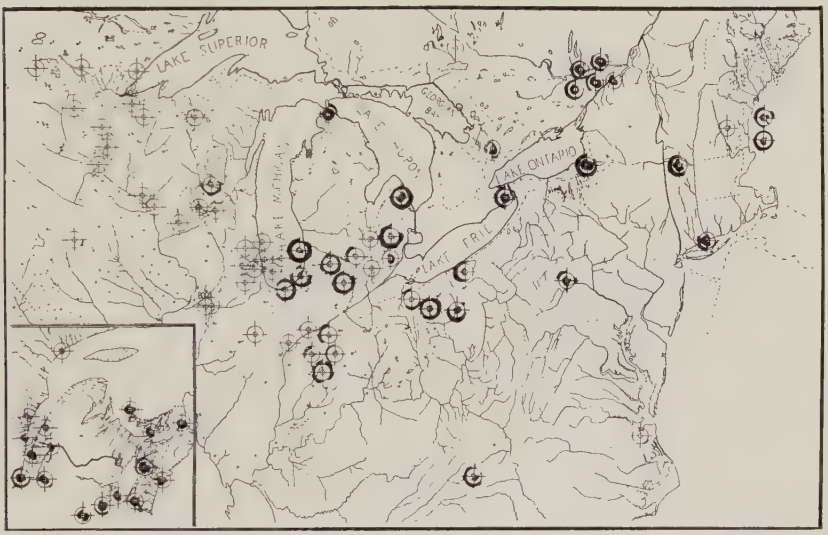

Fig. 4. Clock diagrams showing postglacial changes in frequency of hemlock (inner circle) and beech (outer circle). (From Preston Smith.)

Plotting this data for each genus separately, a series of contours is obtained indicating the direction of its postglacial advance. For graphic purposes, the area in which it was earliest has been indicated in black. This is assumed to represent, in general, the "center" of its postglacial distribution. Except for *Quercus* and *Carya*, the present range limits of each are indicated by a dotted line.

The dispersion of *Tsuga* westward and northeastward from the New England area is apparent from Figure 5. Further pollen analyses, such as the unpublished work of Cain in the South Carolina Piedmont, will shed light on the late glacial movements of this genus north into New England. Undoubtedly former land areas now submerged were involved in this late glacial migration, preceding the postglacial movement shown on the map. For *Tsuga* is well established in the Southern Appalachians and certainly must have been there throughout the Wisconsin glaciation.

Figs. 5–9. Order of postglacial appearance of five important genera. Numbers indicate relative order of each in the series of five.

It is noteworthy that *Quercus* (Fig. 6) was first of the five everywhere except in the region where *Tsuga* had that position, centering about Long Island. The general northward advance of *Quercus* in postglacial times is evident, and in keeping with the size and complexity of that genus.

The diagram for *Fagus* (Fig. 7) clearly suggests a general northerly advance. The presence of *Fagus* in the Arkansas-Oklahoma boundary, and of sugar maple relicts 200 miles further west indicates that the Southwest, as well as the Appalachians, may have been an important place of retreat during glaciation.

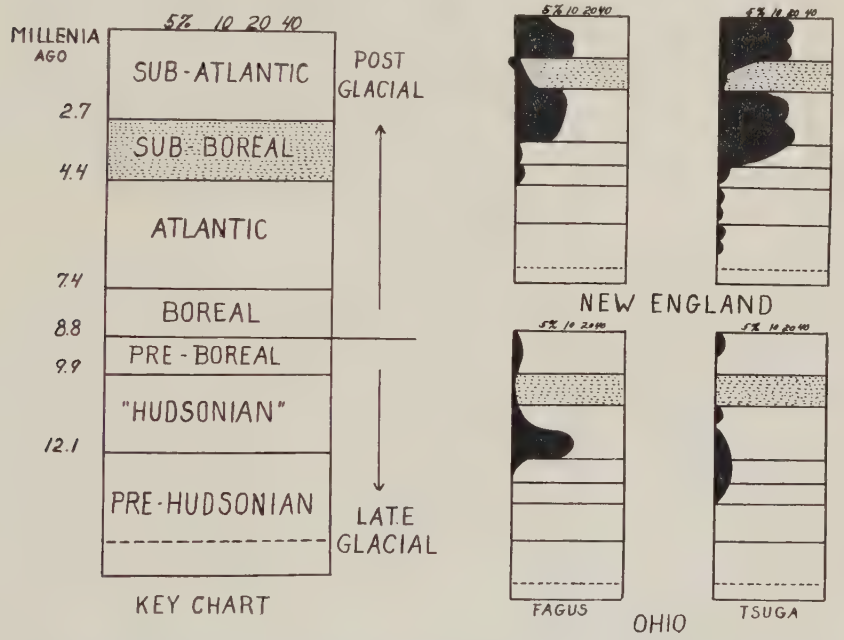

Fig. 10. Correlation of American and European chronologies with sample profiles for *Tsuga* and *Fagus* from New England and Ohio. Note minima for both genera during Sub-Boreal (xerothermic period). (From Preston Smith.)

Moreover a westerly center for *Carya* (Fig. 8) is suggested strongly, but as in the case of *Fagus*, we need more data from places like southern Illinois.

The diagram of postglacial migration for *Tilia* (Fig. 9) shows a definite movement toward the East and South. This also raises questions regarding a westerly glacial refuge. Certainly *Tilia* is today a dominant in the transition forests at the margin of the grasslands in Eastern Nebraska.

Finally I have permission to draw upon the data accumulated by Mr. Preston Smith (18). Using the varve counts of Antevs, north from New England, he has connected bog sedimentation with a definite postglacial chronology. He has also correlated bog reports over a

wide area, having developed a method of plotting a particular kind of pollen in terms of its own frequency.

His scale is shown in Figure 10. For our purpose its most significant use is in confirming the existence of a warm-dry (xerothermic) period, the Sub-Boreal, as well as the general migration facts for beech and hemlock already indicated in this paper. The Sub-Boreal, it will be noted from the figure, is marked by a definite reduction in beech and hemlock, as compared to more xeric forest trees.

SUMMARY

This paper discusses the evidence from pollen analysis which establishes the existence of a postglacial warm dry period in eastern North America. This period has been an important factor in the pattern of present day native vegetation. The migrations within the glacial area of *Quercus*, *Tsuga*, *Fagus*, *Carya*, and *Tilia* are also traced. In general terms, the advance of *Quercus* and *Fagus* was northerly. *Tsuga* was dispersed from the northeast; *Carya* and *Tilia* from the west.

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THE DIFFERENTIATION OF THE DECIDUOUS FOREST OF THE EASTERN UNITED STATES

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Deciduous forest originally covered a large part of the eastern United States. A certain unity is given to the formation by the dominant life form and by some of the wide-ranging genera and species. However, it is not uniform throughout, but differs in different geographic sections in its composition and dominant trees. Why? Because conditions are or have been different in different parts of the area.

Forests develop. Any change in environment causes a change in vegetation. Such vegetational changes are usually gradual and may be local or widespread depending on the magnitude of the causal factor. The reactions of occupying vegetation produce changes, gradual development. Soils undergo modifications hand in hand with vegetational change, from the time of their origin from parent materials, to the ultimate development of mature soil of a regional type. The progress of erosion cycles is accompanied by vegetational change; youthful, mature, and old age stages of the erosion cycle are vegetationally different. The environmental features of the peneplain are different from those of a mountain range or strongly dissected plateau. Continental configuration changes; here coast lines rise and continental shelves emerge; there coasts are drowned and erstwhile parts of continents submerged. Such continental change must result in vegetational change—in migration and shifts in the ranges of species and hence in the composition of communities. Climates change, becoming more humid or less humid, warmer or colder. Every change in climate is accompanied by changes in vegetation and shifts in vegetational boundaries.

The record of vegetational change or development may be preserved in fragmentary communities preserving earlier successional stages, in isolated (relic) communities apparently not in complete accord with existing conditions, in disrupted ranges of species or groups of related species, and in fossils. All of these we must use if we are to trace the changes which have taken place in extent and composition of our deciduous forest.

Differentiation of the eastern deciduous forest is a result of forest development and change in response to these (above mentioned) changing local and regional enviroments, both present and past. The great area occupied by deciduous forest is not all of the same age, nor has it all had the same history.

The Appalachian upland has been continuously available for forest development since the origin of angiosperms, now the most important constituents of deciduous forest. Its central part, especially the western slope of the unglaciated Appalachian upland, is remarkable for the diversity of aspect of its forest, which results from the large number of species and innumerable variations in groupings of species. Here is

preserved a large remnant of ancient forest, of the forest of the Tertiary age. Many of its genera and some of its species are common to this area and to the deciduous forest of Asia, two areas between which there has been no connection since late Tertiary time. Can species persist this long? The paleontological record, although very inadequate for the East, nevertheless gives evidence that they can. There are recognized instances of specific identity of Miocene and existing plants. No adequate picture can be had of deciduous forest without emphasis of its central part, no reconstruction of the history resulting in its present differentiation is possible without a knowledge of this central part, this remnant of, or lineal descendant of, the Tertiary forest.

Mixed deciduous forest occurs throughout the unglaciated Appalachian upland, and to some extent beyond it. However, only in certain parts, especially the Cumberland Mountains and southern Allegheny Mountains, and adjacent Cumberland and Alleghany Plateaus,[1] does the mixed forest that we know as *mixed mesophytic forest* prevail. Vegetationally, this is a forest made up of some twenty or twenty-five species, a forest without definite dominants, or with several important species, rather than only one or two. Slight environmental differences in the optimum area of mixed mesophytic forest result in segregation of its species into more or less well marked communities. Certain of these communities belong to drier sites—ridge tops and steep southwesterly slopes. Others reflect altitudinal influences. But even where altitudinal range is slight and extremes of moisture absent, variations in forest composition occur, and distinct association-segregates may be recognized.

Going away from the center, or region of best development of the mixed mesophytic forest, we find a tendency toward greater uniformity of type; that is, there seem to be fewer segregates in the mixed mesopytic forest. Gradually, in all except a northerly direction, the mixed mesophytic forest becomes more and more limited to favorable sites, lower ravine slopes, coves, gorges. More and more of the area is occupied by some type of forest not readily referable to the mixed mesophytic association.

Let us consider a few forest areas situated on radii diverging from the center of mixed mesophytic forest. This will illustrate the change in composition so evident in all directions.

Southward, in the region of the higher southern Appalachians, the significance of the forester's term, "cove hardwoods," becomes apparent. "Cove hardwoods" and mixed mesophytic forest are one and the same, but here in the mountains of eastern Tennessee and western North Carolina, the mixed mesophytic forest is largely limited to coves. The Joyce Kilmer Forest in North Carolina contains a much higher percentage of chestnut than is found in the typical mixed mesophytic forest. In the Great Smoky Mountains, mixed mesophytic forest occupies the coves and deeper valleys, chestnut is (or rather was) important over a much larger part of the mountain slopes than in the Cumberland Mountains.

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[1]Physiographic regions are used as defined by Fenneman, N. M., Physiography of eastern United States, McGraw-Hill Co., 1938.

Eastward, in the George Washington National Forest in Virginia, on one of the ranges of the Ridge and Valley Province, we find an apparently mesophytic forest tract which is quite evidently the oak-chestnut-tulip tree type distinguished on some vegetation maps. Farther east, on the Blue Ridge of Virginia, we find (in White Oak Canyon) a mixed forest which is about half oaks and chestnut. Both of these forest tracts are in situations in which any one familiar with the mixed mesophytic forest would expect to find that association. Yet both of these, though mixed forests, might be considered as belonging to the oak-chestnut association. In the narrow gorge of Ceder Creek near Natural Bridge, Va., is forest which is definitely of the mixed mesophytic type. Farther east, on the Piedmont, the prominence of oaks is well known.

Southwestward, toward the southern end of the Cumberland Plateau, the slope forest has a lower percentage of the typical trees of the mixed mesophytic, especially basswood and buckeye, and a higher percentage of oaks, although the forest still retains the aspect of the mixed mesophytic forest, and typical stands of that forest occupy the most mesophytic slopes.

Westward, too, we find this limitation of mixed mesophytic to the most favorable sites. For instance, in the gorge of Clifty Creek in Todd County in western Kentucky, there is good mixed mesophytic forest with a high percentage of beech. Forests of ravine slopes in the Mammoth Cave region contain many of the trees of the mixed mesophytic forest, yet there is a pronounced increase in oaks and hickories. In the Ozark region of Missouri and Arkansas, there is no question but that oak-hickory forest is the prevailing association. Nevertheless there are small areas of forest in this region—in canyons and deep valleys—which closely resemble the mixed mesophytic forest to the east.

What is the situation northward? Mixed mesophytic forest extends through the mountains of West Virginia and into Pennsylvania, gradually changing because of the increased importance of maple and beech, and because of an admixture of more northern species, to the northern beech-maple forest or to the hemlock-white pine-northern hardwoods type, or northeastward, to the "mixed transition forest" distinguished by foresters.

Where the boundary of Wisconsin glaciation is reached, whether it be in western New York State or in Ohio, anywhere west of the longitudinal ranges of the Alleghanies, there is an abrupt change in forest composition. Beech and sugar maple at once assume greater importance than in the mixed mesophytic association. The area of the beech-maple climax has been reached. Farther west, in Indiana, there appears to be a division of dominance between beech-maple and oak-hickory, beech-maple generally occupying the more mesophytic sites.

Let us try to reconstruct the events which lead to the present forest pattern. Fossil records show that a broad-leaf forest, with many existing genera, and hence a mixed forest, extended across the now prairie and plains states in late Cretaceous and early Tertiary time. These early forests contained also representatives of many genera not now found in the forests of north temperate regions today, for the climate for at least part of that time was probably milder than now.

Zonal shifts in vegetation, readjustments of species distribution, doubtless accompanied the cooling of the late Tertiary. The Rocky Mountains began to rise (in post-Cretaceous time), and the land to the east of them was deprived of rain-bearing westerly winds. The drying continental interior was no longer suitable to deciduous forest and its boundary receded eastward contemporaneously with the development of the great interior grassland. Increasing aridity in the interior meant the withdrawal of the most mesophytic tree species, while those of lesser moisture requirements found the somewhat diversified topographic conditions of the Ozark Upland favorable. This then became the stronghold for what is now known as the oak-hickory forest. (Other east-west shifts in forest and forest species have of course taken place, at least some of which are Pleistocene or later.)

The mixed forest for the most part retreated to the east of the Mississippi River, although, as has been mentioned, remnants of that forest are seen in isolated situations in the Ozarks, and curiously enough, on Crowley's Ridge, a low ridge of Tertiary age rising above the wide alluvial flood-plain of the Mississippi River.

Cycles of erosion, resulting in peneplains more or less extensive, were affecting the eastern forest area, for slopes change and soils change with the progress of the erosion cycle. Unreduced areas, on an otherwise peneplained surface, afford habitats not general on the peneplain. Hence these sloping areas could have been, and probably were, the most favorable sites for mixed forests similar to those which now occupy slopes. Uplift brings about renewed erosion and renewed soil development. Much of the land surface will again be sloping. Remnants of old peneplains will remain, and parts of newer ones be forming.

The physiographic features of the East are in large measure due to the work of two erosion cycles, resulting respectively in the Schooley and Harrisburg peneplains. Today, over the great area where the upland levels represent the reduced Schooley peneplain, and where no later peneplain was extensively developed, the mixed mesophytic forest prevails.[2] This is an area, for the most part, of mature topography.

The development of a later peneplain—the Harrisburg and its more or less contemporaneous representatives in the interior—again curtailed the area occupied by mixed forests of slopes. Subsequent erosion has considerably dissected the interior representatives of this peneplain, but has little affected the broad valleys of the Ridge and Valley Province.

Cycles in soil development must have more or less paralleled these cycles of erosion. Young soils, showing the characteristics of their parent materials, will cover newly eroding slopes. As time goes on, the soils will become mature, will reach "a stage of development marked by the practical absence of geological features."[3] Such soils, and only such,

[2]Some may wish to include additional peneplains, and assign to the Allegheny or even to the Harrisburg peneplain, the upland levels of the Appalachian Plateau in eastern Ohio. Whatever peneplain interpretation may be followed, the correlation between the area of mixed mesophytic forest and the oldest peneplain of the Plateau remains.

[3]See Wolfanger, Louis A., The major soil divisions of the United States. John Wiley & Sons. 1930.

can support the regional climax vegetation. Soils may become old, and lose some of the essential characteristics of normal soils of their climatic region. Such old soils generally "occupy old flat surfaces of earlier topographic cycles where they have been undisturbed for long periods of time."[4] As most of the former Schooley peneplain has been reduced to slopes, few if any such old soils occur; most of the soils are mature. Many parts of the Harrisburg peneplain, however, are still flat. The forest of these areas in places seems out of accord with the regional type. White oak is the dominant tree.

Glaciation was a major event affecting the forests of eastern United States. Only 30,000 years, more or less, have been available for the revegetation of the glacially denuded land; only a fractional part of this time has been available for deciduous forest development. This is in contrast to the millions of years of undisturbed occupancy of the unglaciated land to the south, occupancy of course affected by cycles of erosion and of soil development. After long developmental stages, climax forests have in places become established in the glaciated territory, although in much of the area development is still in progress, species ranges are shifting. Due to the limitations of climate, of soils, of migration capacities, all of the species involved have not moved equal amounts or at equal rates. The post-Wisconsin xerothermic period favored an eastward movement of the constituents of the oak-hickory forest migrating northward from the Ozark upland. It thus became established in the western part of the now forested glaciated territory. The maximum movement of the more mesophytic species was to the east of the prairie lobe. Thus arose the beech-maple forest, so well represented in parts of Michigan, Indiana, Ohio, and western New York.

Ecologists generally recognize four major subdivisions or climax associations of the deciduous forest: mixed mesophytic, oak-hickory, oak-chestnut, and beech-maple. The areal distribution of each of these is related to climatic and physiographic features, past and present, and the inter-related process of soil development.

The mixed mesophytic association occupies a central position in the deciduous forest. This is a region of moderate to high rainfall, of cold, though not extreme winters. The area of its best development, the Cumberland Mountains and Cumberland Plateau and southern Allegheny Mountains, is an area of mature topography, for the most part the area of the reduced and dissected Schooley peneplain. Within this area the complex mixed forest displays many segregates demonstrating the sensitiveness of its constituents to minor variations in environment—microclimates and soils, both of which are affected by physiographic history. The extent of mixed forest (of which our mixed mesophytic association is a lineal descendant) has been curtailed in the past by climatic changes—increasing aridity in the west, and later, glaciation in the north. Its limits have been modified by the progress of erosion cycles, by the progress of soil development and the establishment of zonal soil types. None of these influences has brought about sharp

[4]Wolfanger, loc cit., p. 13.

areal limits of the mixed mesophytic association. Yet certain correlations may be pointed out. The Allegheny Front, and southward, the Cumberland Front, form the eastern boundary of the area where mixed mesophytic forest prevails. East of this, except in the southern Blue Ridge, the land was profoundly affected by the Harrisburg cycle of erosion. The boundary of the Wisconsin ice sheet forms the northern boundary of mixed mesophytic forest, except that, in the higher longitudinal ranges of the Allegheny Mountains, transitional forest occurs. Roughly, the southern limit of the gray-brownerth, or the northern limit of the red-and-yellowerths, forms the southern boundary of the mixed mesophytic association. This soil boundary reflects a climatic boundary, for the red-and-yellowerths are the result of the open winters of the climate in which they have developed. The red-and-yellowerths are poorer soils than the gray-brownerths and do not support the mixed mesophytic forest. On those poorer soils, oak-hickory forest, or in places oak-chestnut forest prevails. Along the western edge of mixed mesophytic forest is a broad transition belt. There is no zonal soil line, no line related to a past erosion cycle. The climatic limit, in the absence of other factors affecting or affected by climate, is indefinite. Within the area of the mixed mesophytic association, both oak-hickory and oak-chestnut forest occur. That neither is climax in this area is at once evident from the fact that both occupy either immature soil areas, ridge tops or dry slopes on which the soil does not have the normal soil profile, or old soils of a former topographic cycle. Which type is present on a ridge or slope depends upon the nature of the underlying rock—certain evidence that neither is climax in the area of the mixed mesophytic association. In the climatic areas in which these prevail, this relation to underlying rock does not exist. The mull type of humus layer prevails in mixed mesophytic forest.

The oak-hickory association is to the west, northwest, and to some extent to the south of the mixed mesophytic association. The higher rainfall of its southeastward extension is compensated by the poorer zonal soil.

The oak-chestnut forest is, for the most part, to the east and southeast of the mixed mesophytic, although areas of typical oak-chestnut or oak-chestnut-tulip tree forest occur farther west. Throughout the extent of the oak-chestnut association (except perhaps far to the northeast) areas of mixed mesophytic forest are of frequent occurrence on mature soils of valleys dissecting the Harrisburg peneplain, and in coves on the long slopes between the Schooley and Harrisburg levels. This suggests, of course, that the boundary is not climatic, and that the oak-chestnut might be replaced by an extending mixed mesophytic forest. Such extensions have reached the outer edge of the coastal plain.

The beech-maple forest is the northern mesophytic expression of deciduous forest. The transition toward beech-maple demonstrated above 3000 feet in the Allegheny Mountains, shows the climatic relation between mixed mesophytic and beech-maple. The sharp southern boundary farther west, at the boundary of Wisconsin glaciation, is in part historic. This boundary may shift by invasion of additional mesophytic species. Northward, beech-maple gives way to the hem-

lock-white pine-northern hardwoods or lake forest. Westward, the boundary of beech-maple and oak-hickory is approximately the boundary of the prairie peninsula. Past and present climates have affected this boundary.

To summarize: All of the associations of the deciduous forest are genetically related. Within the area of the mixed mesophytic forest, association-segregates suggest the mode of origin of a variety of types from the mixed forest, and demonstrate the relationship of oak-hickory, oak-chestnut, and beech-maple forest to the mixed mesophytic forest. The differentiation which we see today is the result not alone of existing conditions, but also of past history, climatic and physiographic. The more or less gradual change in forest composition, from the area of mixed mesophytic forest outward in all directions, reflects the influence of past and present differences of environment. Transitions between associations are generally gradual, hence boundaries are indistinct. Yet these boundaries may in part be correlated with soil development and the establishment of zonal soil groups; with cycles of erosion; with changes in climate, increasing aridity in the interior and later, glaciation.

Insect Embryology

Much has been written concerning the development of individual insects, but few have been the attempts to summarize the data available. The present volume does not attempt to present all the available data but out of many years experience Professor Johannsen has been able to select judiciously that material which contributes to a clear picture of the field. The able assistance of Dr. Butt is demonstrated in the quality of the illustrations.

The arrangement of materials is unique. Part I is devoted to a summary of insect embryology. Types of cleavage in eggs; a type of embryonic development; fertilization, maturation and cleavage; early development; embryonic envelopes; gastrulation and germ layer formation; the alimentary canal; ectodermal derivatives; mesodermal derivatives; polyembryony; microorganisms in the egg; experimental embryology. These general topics are carefully treated, controversial points are recognized and various views presented. Numerous references to specific papers are appended to each chapter. Part II is devoted to discussion of the embryology of specific insects as representatives of groups. In this portion the whole of Class Hexapoda is surveyed. A discussion of the embryology of Myriapods conclude Part II.

This book is an invaluable contribution to the study and particularly the teaching of Insect Embryology. Both authors and the publishers are to be congratulated upon this notable volume.—*Paul E. Schaefer.*

Embryology of Insects and Myriapods, by Oskar A. Johannsen and Ferdinand H. Butt. 462 pages. New York, McGraw-Hill Book Company, Inc., 1941. $5.00.

RECENT TRENDS IN HORTICULTURAL RESEARCH

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So rapidly do the different areas of plant science change and enlarge that I may be pardoned if I first attempt to express a viewpoint of what horticulture is, and thus account, in part, for the diversity of its activities in modern research.

It is indeed not easy to delineate horticulture, to hit on a definition that adequately expresses the modern concept of the word. One attempts to trace its boundaries only to discover overlappings in other fields, controversial spheres of influence. Yet there is a popular notion of horticulture which brings people to flower shows, to cherry blossom festivals, to the market place. That practical horticulture and research are inexorably bound together is a fact that cannot be ignored. So if I refer to practical matters it is not that I am trying to find a place to hide but because of a patent fact.

It must be obvious to anyone that horticulture has to do with certain kinds of plants or crops which have through long custom been associated with it. Furthermore horticulture represents a special type of viewpoint. This latter is rather intangible but none the less true. In the beginning horticulture referred to a garden, that is, to an intensive type of plant growing in contrast to the culture of field crops. This meant fruits, flowers, vegetables, and ornamental plants. It represented a certain refinement of agriculture which came with leisure or was associated with the home itself. As plantings were expanded for commercial purposes the old idea of interest in the individual plant was retained. Whether apple, potato, or rose farming is still horticulture might be debated by some. But certainly horticulture has emerged from a garden into a vast enterprise and includes such features as nursery practice, the growing of vegetable and flower seeds by the thousands of acres, the processing of canned and frozen foods, the manufacture of spray materials and fertilizers, as well as the growing of fruits, flowers, vegetables, and ornamental plants.

Finally, it must be pointed out that horticulture is both an art and a science. It was an art long before there was any science or any agricultural colleges, and the art will continue whether there is a science or not. It is practiced by the untaught and by those of the greatest learning and culture. That is, horticulture, the art, does not belong to horticultural departments, neither is it destroyed no matter into whose hands it may find itself for a time. It retains its distinctive features, no matter into what university melting pot it may be thrown.

Having expressed this as a background I will attempt to point out some trends in horticultural research. The cases have been selected at random and quite arbitrarily.

THE PLANT'S ENVIRONMENT

If we consider ecology as that branch of biology which deals with the mutual relations between organisms and their environment, then horticulture makes the widest use of it. Ordinarily we do not call the studies by this name, and perhaps a new term will be introduced which will refer more particularly to applied or artificial relationships. Some reference must, therefore, be made to the manipulation of environmental factors, particularly those that are within the hands of the operator. As Livingston says: In all our experiments the environment lurks behind the scenes, as it were, ever ready to baffle our efforts and always calling for very watchful alertness on our part.[1]

The grower of crops must deal with the environment below and above ground. As he changes the environment by cultural practices, whether it be tillage, irrigation, pruning, or spraying, he to some degree affects the plant behavior. Let us look briefly at some of the work along this line.

Temperature.—It is only in the greenhouse and in the refrigerated storage that much can be done about temperature. True, orchard heating is practiced in some sections, mulching is used in part to prevent great fluctuations in soil temperature, but in the main, the horticulturist must select varieties and cultural practices that give the least trouble. Temperature is, however, receiving considerable study and most marked effects are obtained. That temperature has an influence on growth, anatomy, and the metabolism of the plant is manifest.

An interesting and illuminating case of the effect of temperature upon the vegetative and reproductive phases of development is that reported for cabbage. Premature seeding or "bolting" of cabbage is of common occurrence. The cause was usually assigned to poor seed although it was known that early sowing of seed predisposed the crop to this trouble.

Work conducted under the direction of Thompson[2] at Cornell showed that "mature plants taken up in the fall before they were subjected to low temperature did not seed when grown subsequently in a warm greenhouse (60° to 70° F.), while those grown in a cool greenhouse (50° to 60° F.) produced flowers and seed. The plants grown continuously in the warm house produced three heads in succession during the first year. One of the plants was kept in the warm house for two years after it was brought in from the field in October, 1925, and this plant produced six heads. After the sixth head developed and the plant was about three years old it was moved to a cool house and within a few months it flowered. The plants used represented a pure-line strain so that all of them had the same genetic constitution."

The opposite of this situation obtains with lettuce, high temperatures favoring premature seeding.

In none of these cases has length of day been a factor.

With greenhouse plants grown for their flowers, equally interesting results have been secured. For instance, stocks, which also belong to

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[1]Livingston, Burton E., 1934. Environments. Sci. 80: 569–576.

[2]Thompson, H. C., 1939. Vegetable Crops. McGraw-Hill Co.

the Criciferae, respond very similarly to cabbage, but since it is the flowers that are wanted the early "bolting" is desirable, and subjecting the seedling plants to low temperature may now be practiced.

Bulbous plants also are treated to force early flowering. Daffodils and bulbous iris subjected to 50° F. before forcing will bloom about four weeks early. If tulips are first preheated at a low temperature of 75° to 80° F. and then subjected to a low temperature they can be advanced considerably in time of bloom. This work has been done in Holland, England, and America. Darwin tulips can be secured in this manner in November instead of February as had been customary.

Lilies do not initiate flower primordia in the bulb stage as do other bulbs; hence it is possible to subject the young plants when a few inches high to a temperature of 50° for about two weeks. Such treatment will increase the number of buds per stock.

If gladiolus corms are placed in a temperature of 75° to 80° for a month before forcing, that is, preheated, they will flower about a month early.

Equally striking anatomical differences may be noted at different temperatures.

Water.—Water is such a commonplace that one would not expect to pay attention to it unless there was a great surplus or deficiency. Yet a successful greenhouseman will tell you that one of the most difficult operations to teach to a beginner is that of watering the plants. The desired amount varies with the kind of crop, the weather, the season of the year, the stage of development of the plants, and the nature of the soil. Many a crop is ruined by the misuse of water.

We have always thought of water as "water," but there are those who say that now we must unlearn that. Quoting Professor Salisbury: "Much of the water we drink is not simple water, but double water composed of two H_2O groups linked together as dihydrol. What constitutes water in the state of ice is not known, but when ice melts the water which is released is neither simple H_2O nor the double brew, but is composed of three molecules linked together as trihydrol. Whether these variations on the simple watery theme have any significance in horticulture cannot yet be stated with certainty. It is true that when plants are watered with what is simple water, as, for example, water from condensed steam, they do not, so it is said, grow so well as when they are watered with melted ice water. . . . It is often claimed by gardeners, and probably the claim is sound, that heavy falls of snow have a beneficial effect on the subsequent growth of plants."[3] And so the simplest elements of the environment are in for re-examination in the light of their effect on plants.

An interesting case of research in regulating water supply is provided in studies with tomatoes. Limited watering which allows the soil to be alternately wet and dry results in a large percentage of the crop (more than 75%) being affected with blossom-end rot, whereas similar plants which are kept well supplied at all times show practically none of this trouble. In fact, this simple treatment has practically eliminated it from greenhouses.

[3]The plant and its water supply. 1938. Gard. Chron., March 19.

Light.—Following the classic work of Garner and Allard on the effect of length of day on plants, the horticulturist has made some practical use of this finding, notably with greenhouse crops. The chrysanthemum, being a short-day plant, was particularly amenable to treatment. Laurie and his associates[4] used black cloth to cover the beds in the greenhouse from 5:00 P. M. until 7:00 A. M. each day for a period of 30 to 35 days beginning July 15. This treatment has advanced the crop a month or more. On the other hand using electric lights to lengthen the day delayed flowering so that the mum season is now six instead of the usual three months.

Similarly, asters may be brought into bloom earlier by shortening the daylight period.

Just as shortening the day has induced early flowering of certain plants, so lengthening the day has had equally beneficial effects with certain other commercially grown flowering plants. The additional light should be applied from 5:00 to 10:00 P. M. or from 2:00 A. M. to 7:00 A. M. during fall and winter. Particularly responsive are *Lilium longiflorum,* annual chrysanthemum, *cineraris, Gypsophila,* and stocks.

Atmosphere.—It is not easy to regulate the atmosphere about plants and perhaps as conspicuous an example of efforts in this direction as might be cited is the use of modified atmospheres for the storage of fruit, or gas storage, as it is called in England. Trials have been made for years on the effect of artificial atmospheres in the storage and transit of fruits. As early as 1821 Berard was presented with a medal by the French Academy of Science for his paper on the storage of fruit in atmospheres devoid of oxygen, but it is only within the past few years that interest in the subject has developed from a commercial standpoint.

Smock[5] has described this type of storage and the results procured by it. He points out that respiration is diminished in intensity not only by lowering the temperature but also by reducing the amount of oxygen or allowing CO_2 to accumulate. Yellow Newtown apples held in CO_2 concentration of 10 per cent at a temperature of 45° F. were as green and firm as those held in air temperatures of 32° and 36°. Northwestern Greening apples after 30 weeks in 5 per cent CO_2 and 2.5 per cent oxygen (normal is 21 per cent O_2) at 40° F. were still as green as when first stored. Comparable fruit stored in normal air at 40° for the same period was completely broken down and worthless. Similar fruit stored at 36° was wholly unmarketable after 30 weeks because of softening, yellowing, and 100 per cent brown core. Excellent results were secured with McIntosh and other kinds of fruit.

I need scarcely call your attention to this work as pointing to a new method of commercial fruit transportation and storage.

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[4]Poesch, G. H., and Laurie, Alex. 1935. The use of artificial light and reduction of the daylight period for flowering plants in the greenhouse. Ohio Agr. Exp. Sta. Bull. 559.

[5]Smock, R. M. 1938. The possibilities of gas storage in the United States. Refrig. Eng. Dec.

The Soil.—So extensive is the work with soils that I can only touch on a few trends.

Probably the most conspicuous to those of us who have been associated with horticulture for a good many years is that of soilless culture or hydroponics, as it has come to be known in some quarters. The very thought of growing crop plants to maturity without soil, without organic matter, is rank heresy. If I had not been in the midst of this work for the past few years I too would smile. How extensive it will become cannot be said, but the fact is that better quality flowers are being grown in a medium of gravel, cinders, or a similar inert material than in soil. In some cases the yields are also higher. For instance, 35 rose flowers are being produced per plant in gravel culture and 20 is the usual number in soil. Sweet peas average about 50 per cent more in gravel. Carnations produce no more cut flowers in gravel, but the blooms bring a premium on the market because of their quality. The same may be said of snapdragons, calendulas, stocks, lilies, daffodils, iris, and many annuals.

Among the vegetables, tomatoes are having a wider trial than others and there is some reason to suppose that they may be grown profitably without soil.

Among the advantages of this system of culture are better aeration, uniform moisture conditions, better control of soil-borne diseases, a better balanced condition of the nutrients, and control of the reaction of the medium.

Quoting an English reaction to soilless culture we see what is a somewhat facetious quip. "Of course, it is only right and proper in a commercial age to prove all things and hold fast to that which is cheap! Of course, it is very attractive for anyone with a love of the picturesque in prophecy to foretall the time when the soil of North America—and elsewhere—having slipped away in the sea or blown away into the air, the teeming millions of that and other continents will be sustained by the produce of the Great Lakes. The charm of Lake Superior and all the rest of them covered with crops! Waving fields of maize and wheat and all kinds of vegetables, all growing in and out of the water! We, for our part, however, would rather exercise our imagination in picturing how happier and healthier we should all be if research could discover how to make the earth more fertile."[6]

Turning more directly to the soil itself there are several factors that are being studied with profit and which have a much wider application, although not so spectacular as soilless culture.

Perhaps no phase of the soil factors has been so blandly discussed as the role of organic matter. I would not want to jostle this eternal verity from its throne in agricultural science, but it seems to me that some of our early teachings were pretty much fairy tales in the light of recent findings. That organic matter is built up as a bank account by the return to the soil of large quantities of manure or cover crops to be drawn on by the tree at some future time, has not stood the test of investigation. Referring to orchard soils in particular, it has been

[6]Growing plants without soil. 1938. The Gard. Chron., Dec. 3.

found that the growing of green crops which were turned into the soil has resulted in a net loss of total organic matter as compared to land which was left in sod or where the trees were mulched. At the Ohio Station we find, after 25 years, that the tilled land has 1.8 per cent organic matter as compared to 3 to 5 per cent under sod and mulch. Tillage of orchards on rolling land has been a fallacy which has resulted in untold loss of soil and ruination of its physical characteristics which many years of intelligent husbandry will not restore.

Another result of recent studies has been the value of porosity or the movement of air and water through soil. The importance of this matter had been recognized for a long time, but not until the comprehensive work of Oskamp and other horticulturists at Cornell and elsewhere, had its real importance in the life and productiveness of an orchard been measured. The value of aeration in a soil has moved from its sacred place in the laboratory to a most vital position in agricultural practice. The curse of a compact soil, whether natural or brought about by injudicious culture, even in the name of a soil-building program, cannot be overestimated. I am here tempted to quote the familiar lines of Pope:

Where grows? Where grows it not? If vain our toil
We ought to blame the culture, not the soil.

We should not have expected Pope to know that the physical characteristics of a soil are of more importance than the system of culture for orchard purposes, but some who recently quote his lines with approval should know better.

With this we shall reluctantly leave an absorbing phase of horticultural work which is essentially ecology, and look briefly at some other areas of present day research.

PHYSIOLOGY

The importance of physiology in the minds of horticulturists can be measured by the number who take their basic training in this field and immediately engage in investigations in which this science provides most of the tools. To even catalogue these researches would be as impossible as undesirable in this connection. It seems even more difficult to determine just what does and what does not belong in this category.

Perhaps the investigation which stimulated more thinking and additional work than any other was that of Kraus and Kraybill on the relationship of nitrogen complexes and carbohydrates on the flowering of plants. In this the plantsman found a way of thinking about plants, something he could take hold of and manipulate to his purposes.

The discovery of deficiencies of so-called rare elements, such as boron, manganese, magnesium, copper, and zinc has opened a renewed interest in nutritional studies and some important progress has already been made.

Notable in the physiological studies is the development of apparatus for the study of carbon assimilation by leaves in the field and under controlled conditions, by Heinicke and his associates. This type of

apparatus affords a means of conveniently determining the photosynthetic activity of leaves which have been sprayed with various materials and of leaves which are being attacked by insects and diseases, for determining the respiration rate of plants and their products at varying temperatures and with different amounts of light. Horticultural practice has already been influenced by these findings.

From the standpoint of an orchardist, the problem of securing higher color on fruits is of serious moment, especially since the use of nitrogen as a fertilizer tends to prevent the development of sufficient red color for highest market value. Chemical and experimental evidence shows clearly that a high foliage-fruit ratio favors high color provided the synthesis of nitrogen and carbohydrates into amino and protein complexes does not deplete carbohydrates. That is a ratio of 20 leaves per apple gives a lower sugar accumulation and a poorer development of color than 75 leaves. Expressed in orchard terms, the thinning of fruit results in higher color than occurs when a tree bears an excessive crop. These matters are within the hands of the orchardist but the situation is still not satisfactory. Very recently Dustman and Duncan have published results of spraying trees with soluble thiocyanates. The foliage is subjected to spray burn and to a chlorotic condition arising from the effect of the chemical on the green coloring matter of the plant, but in the fruit, the amount of red color occurring normally tends to be increased and the ground color tends to be reduced or replaced by varying shades of yellow and yellow green.[7]

Gardner, Marth, and Batjer[8] have demonstrated the value of certain plant growth substances (hormones) as capable of preventing abscission of various plant organs, including leaves, flowers, and fruits. This discovery has been put to practical use in delaying the preharvest drop of apples by spraying with dilute solutions of naphthaleneacetic acid. The commercial effect of increasing color of fruit as a result is yet to be worked out, but appears promising.

Other work with hormones and vitamins is in the limelight at the moment. The discoveries and the techniques used in the discoveries represent an epochal advance in the knowledge of plants and the forces that direct plant behavior. As might be expected, there are some exaggerations of what may be expected from these discoveries; on the other hand, some of the possibilities arising from these findings would be difficult to overstate. I refer particularly to the use of naphthaleneacetic acid in the production of seedless fruits of tomato, cucumber, and other fruits, not so much because the fruits are seedless, as because of the possibilities of getting a crop of fruit once the flowers are formed even though the pollen is not viable, as often happens in the greenhouse. I refer also to the use of acetylene and ethylene in controlling flower formation as demonstrated, for instance, with the pineapple in Hawaii and Australia where the entire harvesting period has been regulated.

The use of growth promoting substances in the rooting of cuttings

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[7]Dustman, R. B., and Duncan, I. J. 1940. Effects of certain thiocyanate sprays on foliage and fruit in apples. Plant Phys. 15: 343–348.

[8]By correspondence.

seems to be over rated from a commercial standpoint, as does the use of Vitamin B_1 for plant growth.

ULTIMATE OBJECTIVE IS QUALITY

With our typical stress on bigness and quantity, it is not strange that agricultural experiment stations have largely neglected quality except so far as there are dollar signs on it. A healthy, sturdy race of animals and men has not received first consideration. True, we have known that man and animal were dependent upon the products of the soil, have even recognized in a general way that "man was three parts water and one part concentrated grass," but to study the exact composition of these products from the standpoint of proper nutrition, not much was done, at least for man.

QUACKERY

I dislike to conclude with any remarks on quackery, but something akin to this is constantly in the picture and might as well be admitted. The fertile field for lurid colors, get-rich-quick schemes, for magic, wizardry, and the supernatural is probably a result of the large number of amateurs who engage in some sort of plant growing. The doctor, lawyer, and Indian Chief, alike, fall for the fabulous tales of an expert salesman; and, I regret to say, often the experienced greenhouse man, orchardist, and gardener are rivalled perhaps only by the golf greenskeeper as suckers.

Just recently I received a gallon can of Reico, which when sprayed on apple trees "will change the biennial bearing habit!" Other proprietary products now on the market, some with merit, others of doubtful value, are: transplantone, auxilin, vita-flor, hormodin, root-tone, bloomlife, fruitone, and, of course, vitamin B_1. We must admit that if science comes, the commercial adventurer will not be far behind.

With all this, experiment stations and colleges still have ample work to do if the real merit of new products is to be determined and the innocent public protected.

The Great Naturalists Explore South America

It is unusual to run across a book on natural history written for the layman, which is both entertaining and authentic. The Great Naturalists Explore South America is a volume which conforms to the above standards. It consists of two parts. Part I gives an historical account of the naturalists who have traveled in South America. These include Humboldt, Boupland, Waterton, Darwin, Schomburgk, Edwards, Wallace, Bates, Spruce, Hudson, Pritchard, Beebe and Ditmars.

Part two consists of thirty chapters, devoted to descriptions of various animals peculiar to South America. There are forty excellent photographs of many of the animals discussed. Samples of interesting chapters are those dealing with the Vampire Bat, the Jaguar, Hummingbirds, Giant Boas, Electric Eels and Insects as Food. A five-page bibliography is included. We highly recommend this book, not only to the general reader, but also as a stimulating reference for Zoology students.—*D. C. Rife.*

The Great Naturalists Explore South America, by Paul Russel Cutright. 340 pp. New York, The MacMillan Co., 1940. $3.50.

Plant Galls

This book is a revision of the author's earlier work "Key to American Insect Galls," New York State Museum Bulletin, 200, 1917. About 2000 American galls are recorded, classified according to the plant families. Skeleton keys are used within the families, keys which are too incomplete to make ready identification possible. In the oak group, the reader is often abandoned to a list of 20 or more forms from which he must make a choice by reading descriptions.

A far more serious defect in this account of plant galls is the highly inadequate treatment of the biology of galls in the introductory chapter. No mention is made of Kuster's classification of gall types, though Kuster is the world authority on gall structure. The introduction of evolutionary concepts into the field of the higher galls has been totally neglected together with the theoretical application of the recent data on "organizers" which seems applicable in these studies. The most significant literature in these fields has been ignored.

It is unfortunate that the extensive bibliography of the earlier work could not have been included in this new edition, since the earlier bulletin has long been out of print. Only 18 references are given.

To any one interested in expending his acquaintance with animal induced galls, this book is about the only work to which he can turn to find a summary of the American forms. It, thus, should be represented in every biological library.

—*B. W. Wells.*

Plant Galls and Gall Makers. E. P. Felt. 364 pp. Comstock Publishing Company, Ithaca, New York. 1940.

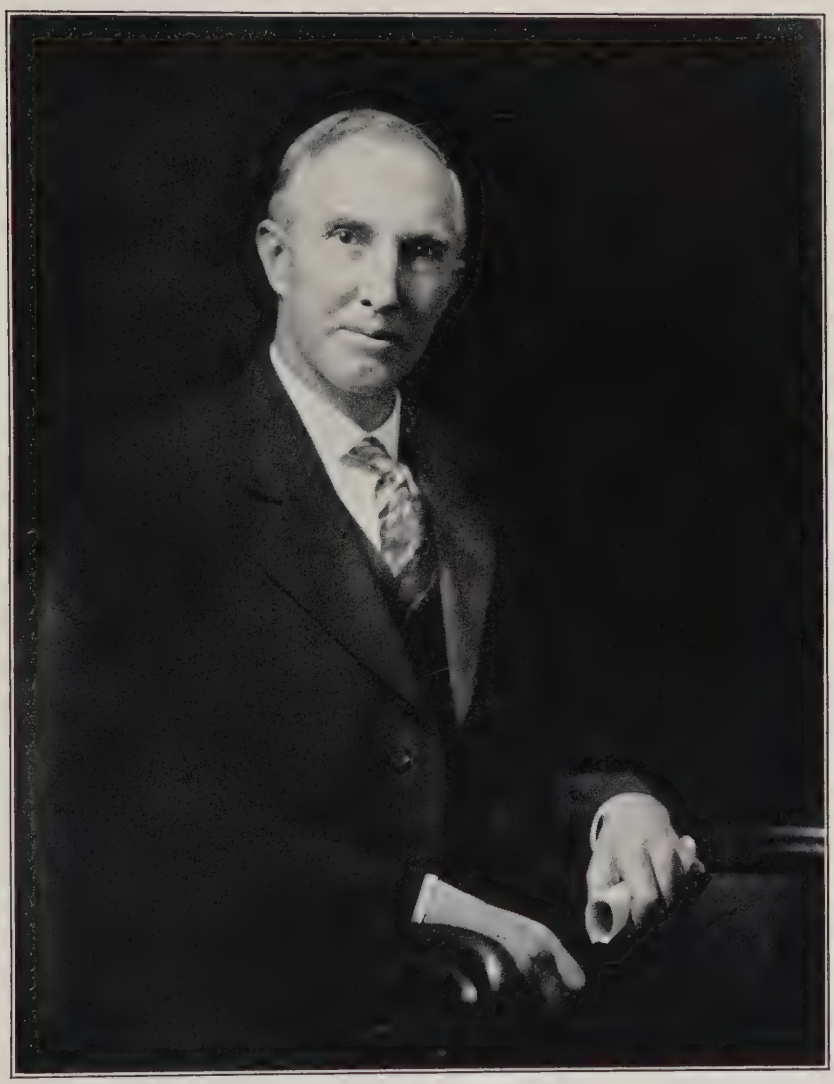
Is There Life on Other Worlds Than Ours?

Probably no other scientific question has been asked so often as has this one and probably no other question has received more unsatisfactory answers. In consequence, human imagination has soared and cheap fiction has prospered. The facts involved in the answer to the question are extraordinarily difficult to assemble in such form that a satisfactory answer is possible. No less a person than the Astronomer Royal of England now makes the effort and has done it exceptionally well. To be sure, the question is still unanswered as it must inevitably be for many years to come but here, at least, is a sober, understandable discussion of the elements and difficulties involved in the answer.

Mr. Jones discusses first the physical setting, then the conditions necessary for life as we know it, then goes on to a critical examination of the methods and limitations of investigation. This last discussion should be of particular interest to any one who wishes to understand why the question still remains unanswered. He also reviews the conditions that probably exist on the planets and comes to the general conclusion that on Mars life, if any, must be nearly done and on Venus it may be just beginning.

The book is well illustrated and interestingly written. There is an unfortunate error on page 37 in the chemical formula for sugar which has one atom of oxygen and one atom of hydrogen too many but this in no wise detracts from the value of the book. The reviewer heartily recommends this book to those who would like to see this problem as it stands today.—*C. E. H.*

Life on Other Worlds, by H. Spencer Jones. X*X*299 pp. with 17 plates. The Macmillan Company, New York. 1940.



JOHN HENRY SCHAFFNER

(1866—1939)

PROFESSOR JOHN HENRY SCHAFFNER

ADOLPH E. WALLER,
Ohio State University

BOYHOOD BACKGROUNDS

A small boy herding cattle in a vast expanse of prairie may not seem important. Doubtless many small boys have engaged in that not too difficult task. They have fought flies, chewed straws, and tried to amuse themselves, perhaps thoughtfully. Most of them have just sat by, waiting until it was supper time and the end of the day's labors. It was lonely to some, boring to others, perhaps exhausting their patience to know that they were prisoners tied to the cattle they were to guard. Most such boys would not think of themselves or of their jobs as offering much. Yet to a mind alive with curiosity such a contemplative life presents rich possibilities. If a landscape is somewhat bare, or at least simple, the individual objects take on a new significance. To a mind eager to question, each rock, each dip in the terrain, each stream requires exploring. With the passing of hours and months, the seasons take on a perspective. With growth of plants the lengthening stems and spray of bloom unfold mysteries that demand investigation. What wonder that the dense prairie sod with its complex and teeming life should hold a world for a small boy's mind!

Such a boyhood background in Professor Schaffner's life circumscribed the making of a great mind. He was born in Marion County, Ohio, near the Agosta prairie, with forests enclosing it, but his family moved early in his life to Clay County, Kansas. The prairie area he had left in Ohio was a mere patch of grassland, an island of grass in a landscape of trees. In Kansas it was different. Grasses and grassland forms reached across the horizon, only interrupted where pioneers had planted some trees near their homes or along streams where a narrow strip of woodland marked the water course. Grasses and cattle were his companions in the long hours he had to remain at watch. Why the flatness? Why the great stretches of sky? The work of the glaciers was still a new idea and probably not mentioned in his school. His parents were busy and perhaps had no time for such wonders. Yet these were the thoughts uppermost in the boy's mind. Geology became his first love in science, though he was far from any one who could talk much about it and had few books that could help him. But no lack of training or of encouragement from the circumstances in which he grew up could take away the desire to know all he could know of the grasslands around him. It would seem that the great expanses of prairie in which he was so small must have left him with a sense of his own obscurity. In later life his modesty never permitted his own great accomplishments to affect him. Like the small boy of the prairie, he was there, ready to speak or to act if any one was interested. But as with the small boy on the prairie, only a few came his way. He never learned to shout to

attract the attention of others. The lonely life with the silent cattle also gave him a sense of his own competence. He was obliged to rely on himself. He formed the habits of self-dependence. He would act if he thought he was right. Having once made up his mind, nothing could move him to change his opinion as long as he thought he was right.

During the early days in Kansas the Schaffner family had to contend with the handicap of poverty. The house was the sod house familiar to many pioneer families of the grasslands. After working two years, the family had accumulated resources sufficient for the father to make a journey to Leavenworth, where a supply of lumber to build a more comfortable frame house was purchased. The lumber was paid for, but before the house was finished a raging prairie fire consumed it all. The Schaffner family, coming from Ohio, had not learned the precaution of plowing furrows to stop fires around the site selected for their wooden farm house. They were obliged to live for two more years in the sod house before again having enough money to buy lumber. This time the necessary strips of plowed land were prepared. After that, although there were a number of prairie fires, the house and the family were safe. In a reminiscent mood Professor Schaffner told this story to several members of the Botany Department staff as he recalled some of the exciting experiences of his boyhood.

Not only was the first Schaffner home of sod, but the earliest school house in the Clay Center area was a bank-sod house—a sort of basement structure. The walls and the roof cover were of sod. This was the school the elder sisters attended for several years. John spent most of his school years in a frame school house. It was a one-room building that served also as a social center, and in it were held the meetings of the debating society, the spelling matches, the Sunday School, and the box suppers. These were the pioneer's fun. There was one other—community singing. Schaffner was musically inclined. He was the only one in the school who could play the organ. He must have enjoyed this and talked about it for his parents at one time considered helping him to study music as a career.[1] This may have been in his college days, as Mr. Thomas A. Evans, Alumni Secretary of Baker University, Baldwin, Kansas, states that while Schaffner attended Baker he was in charge of the music at the Presbyterian Church and adds that Schaffner was gifted in playing the piano and organ and wrote poetry as a hobby.

The Schaffner family in many ways showed ingenuity and originality. The boys made mechanical wooden toys, and even a primitive *camera lucida*, which was set up for reflecting pictures on a screen. These amusements and visiting the neighbors occupied the long winter evenings. The parents were helpful in guiding their children toward instructive recreations.

Mr. D. C. Schaffner wrote: "By the time John started to high school it was taken for granted that he would go to college. Although the two older sisters taught school for a number of years after high school, they did not share this ambition for themselves but assisted

[1]This fact and much of the material at this point was kindly furnished by Mr. D. C. Schaffner, the younger brother, now Professor of Geology at Emporia College.

John and my younger sister and myself in college and graduate schools after each of us had taught in country schools. We formed a sort of teaching-and-going-to-college relay team." Of John, his brother wrote that "he was reticent but friendly. As far back as I can remember he never showed all of himself to anyone."

Science training was in a chaotic condition when young Schaffner at last was free to enter college; training in the classics was the only kind of education available in most of the colleges in the period from 1880 to 1900, and Schaffner's experiences were no different from those of many young men of his day. He was later to have a particular use for his knowledge of Greek and Latin in his scientific work. The classical tradition gave him a most careful training in the exact derivation of words, and his papers never contained new terms that were a polyglot mixture of Greek and Latin. His interest was captured by natural science, and it was geology that he first thought of pursuing.

As a further tribute to the Schaffner family it should be remarked that while the farm never was a source of wealth, it produced sufficient means and talents to be called remarkable. The younger sister is a noted attorney in Chicago; the younger brother, a geologist. The children were not bound down to the pioneer environment.

Probably the greatest inspiration toward research in botany for the boy John came from Dr. Charles Sylvester Parmenter, who was the teacher of biology and geology at Baker University. Dr. Parmenter was doubtless helpful also in securing for the young graduate of Baker University the job of teacher of natural sciences in the Methodist College at Mitchell, South Dakota. With all the delays of his high school and college years, John Schaffner was twenty-eight years old at the time he went to South Dakota. By then his path toward modern scientific study seemed to have become clear to him. After a year at the college at Mitchell he resigned his post to take up graduate studies at the University of Michigan. He remained for two years at Ann Arbor, where, under the guidance of Dr. Frederick C. Newcombe, he began intensive work in cytology.

He plunged at once into the most controversial subject of the moment, the question of cell organization at mitosis. His first paper dealt with the attraction spheres and centrosomes, present outside the cell nucleus, considered from the standpoint of their possible function during karyokinesis. This was a deep and difficult subject for a young research student to undertake. It was all the more ticklish from its didactic nature, since the most distinguished European cytologists were at that time at odds over their discoveries. Young John Schaffner had to master a reading knowledge of French and German to prepare his paper, since of the thirty-five references which he lists only two are in the English language.

THE YOUNG BOTANIST

While we know that Professor Schaffner was engaged in teaching the natural sciences at Mitchell College in South Dakota, we have been unable to trace his associates or to learn much of his development during the two years (1893–94) he remained in South Dakota. He published

his first two papers after he had gone to Michigan. The one on the centrosomes was published in 1894, the other on the embryo sac of the water plaintain, *Alisma plantago*, in 1896. Both came out in the *Botanical Gazette*, which was at that time undergoing revolutionary improvements as a scientific journal. Dr. Coulter, its editor, had just been called to Chicago by President Harper. Dr. Spalding, head of the Department of Botany at Michigan, was on very friendly terms with Coulter, serving as an associate editor of the *Gazette*. Young Schaffner's papers were approved by both Spalding and Coulter, and appeared in the *Gazette* just as it was being revised and expanded. It is significant that young Schaffner came in with the first wave of the swelling tide of interest in botany in the United States, a tide, the level of which was greatly raised by the Chicago group of botanists.

It was at Chicago that the young scientist really began his intensive training in botany. He was attracted by the work of Dr. John M. Coulter and the *Gazette*, where his first paper had appeared. Coulter's success with the old *Botanical Gazette*, of which he had been editor while at Lake Forest College, had been marked. His co-editors, Charles Barnes and J. C. Arthur, were still loyal, but when the University of Chicago with its rich Rockefeller endowment, was behind it, it could make the necessary expansion. Dr. Coulter chose carefully when new associate editors were added—Atkinson of Cornell, Thaxter of Harvard, Spalding of Michigan, and Trelease of the Missouri Botanical garden. These were impressive names, and the quality of the materials Coulter proposed to publish made the new editors willing to lend their prestige.

By 1897, its success having been noted abroad, and Dr. Coulter having had a chance to visit Europe, foreign associate editors were added. The beginning of the great botanic center that was to make the University of Chicago famous for so many years was a reality. The new names made the editorial board of the *Gazette* a roster of botanists of first rank. They were De Candolle of Geneva, De Toni of Padua, Engler of Berlin, Guignard of Paris, Matsumura of Tokyo, Noll of Bonn, Marshall Ward of Cambridge, Warming of Copenhagen, Wittrock of the Academy of Sciences of Stockholm. The editorial staff in the main had no duties, of course, but their names were on the fly-leaf of the *Gazette*. Coulter and the staff of the University of Chicago and the graduate students in botany, who by this time numbered ten or more, contributed much of the materials. The graduate students were not unworthy to contribute to the *Gazette*. Most of them became distinguished professors of botany. In the famous paper on *Lilium*[2] Dr. Coulter names nine, of whom Otis W. Caldwell, Henry C. Cowles and T. C. Frye are perhaps the best known. Coulter did not include the names of Charles J. Chamberlain and John H. Schaffner in this list because Chamberlain and Schaffner independently produced the papers on the pollen sac and the macrospore nucleus of Lilium which were the features of this paper and to which Coulter's contribution was mainly the introduction and the organization of the materials to be studied. In

[2]*Botanical Gazette*, Vol. 23, p. 412.

spite of its being thus buried, Schaffner's studies were the important ones and the ones which today are referred to as the beginning of the evidence in plants for the studies in Mendelism and heredity. Schaffner's paper should have been published as a separate contribution. Everybody knows that now. For it was not just more details in cytology. It was the one idea that the botanists, especially the geneticists, needed.

But Schaffner knew what he was doing. In his introductory sentence he said so. "Although a knowledge of the changes which take place in the reduction nuclei of plants and animals is of the utmost importance and will no doubt aid more than anything else in bringing about a correct interpretation of the facts of heredity, comparatively little has been done in this field, and the observations that have been reported disagree widely." There it was. He had done it, but it disagreed with earlier reports on chromosome behavior. Even Professor Coulter was afraid of it. The conclusion was too startling. And it was so unlike the conclusions of the European laboratories, which so authoritatively dominated the scene. Could it be that young Schaffner was right and some older famous heads were wrong? Let us quote some of the statements from the paper on *Lilium:*

> "Thus there is an actual transverse division of the chromosomes, the half of each original chromatin loop passing to opposite poles of the spindle. Each daughter nucleus, therefore, receives about as many chromatin granules as there were in the mother nucleus, and although there is no diminution in the number of chormatin granules, only half of the granules originally present in the mother nucleus are represented in each daughter nucleus. It will be seen that although the chromosomes are not all of the same size and length, yet if the chromatin band breaks at practically the middle point each daughter nucleus receives about the same number of chromatin granules; and since the chromatin granules are the same in number as in the mother nucleus it cannot be proper to speak of a reduction in the amount of chromatin, although only half of the original chromatin granules are represented. There is no reduction in number but a reduction of one-half in kind."

Whether Dr. Coulter approved or not, the paper had to be presented as a continuation of the morphological and cytological studies in progress, since a whole year's work was involved. But what would some of the foreign associate editors think of it? Was this young man too brash? He seemed quiet enough, but he could not be shaken in his conclusions, and the idea was startling. Now, forty-two years after it was published, we may say that Schaffner did not know he was supposed to agree with the European cytologists so he disagreed. We also may understand that since it was but a section of the planned program of *Lilium* studies it did not have the chance to attract the attention it deserved. It was true that it contained the history of the embryo sac, as the title might suggest. But it contained the startling observation of both a longitudinal and a transverse separation of chromosomes during meiotic processes. It was this type of division which was needed to

account for Mendelian proportions in offspring that botanists were soon to be looking for. Schaffner was the first botanist to see it. Since the main point was not fully emphasized, the credit for this first observation was not entirely awarded to young Schaffner. But if he was disappointed in this, he had no time to fret. For the following year he was called to Ohio State and began the development of a career which was to last for forty-two years.

THE OHIO STATE UNIVERSITY BOTANICAL LABORATORY

The young assistant in the Department of Botany was chosen by Professor William A. Kellerman, who had himself been for a number of years at the University of Kansas before coming to Columbus. Dr. Kellerman was broadly trained and a ready lecturer, with a special interest in mycology. Mr. Schaffner was to assume responsibility for as many of the other phases of botanical science as he felt inclined. None of them was organized. The trails needed to be blazed by pioneers in every department. But few institutions would be fortunate enough to get young men who could blaze trails in so many different directions.

Before assuming his duties at Ohio State Mr. Schaffner returned to Kansas. This annual journey in the summers to Kansas became a fixed pattern in his life, and while no complete record exists, he probably missed few summer visits to his home. In 1897 we have a record for this summer that he visited Cloud County, Kansas, and devoted his studies to the salt marshes. He lists the plants inhabiting the marked vegetation zones around the margins of the marsh in a contribution to floristic ecology. Not only is it recognized today that this pioneer paper on the floras of our inland salt marshes is a valuable scientific record, but it is also Contribution Number One from the botanical laboratory of Ohio State University. This paper appeared in the April, 1898, number of the *Botanical Gazette*. Before this, even Dr. Kellerman, who founded the *Journal of Mycology* and was for many years a contributor to it, had not thought of the device of crediting the Ohio State University's support of his efforts. At that time, of course, Professor Kellerman was already a man of high professional reputation. He had influenced many students, both in Kansas and in Ohio, and played an important part in the development of the work in plant pathology, which was to rise so brilliantly in the Department of Agriculture just organized at Washington—where, later, his son was to become the head of the work in plant pathology. But the plan of crediting the institution which was paying his salary had apparently not occurred to him. His young assistant in botany was to give Ohio State its appropriate recognition. It is symbolic of the fact that Schaffner was entering whole heartedly into a plan of life that was to bring forth every effort in the development of his chosen field.

In 1892 Ohio State University had a new Dean of Agriculture. Professor Thomas F. Hunt, who had previously held the chair of Agriculture at State College, Pennsylvania, was called to the post to succeed Doctor Townshend, who had just retired in his seventy-seventh year. At the same time, the Department of Botany and Horticulture was divided. Professor W. R. Lazenby, who had long held the double title,

was elected Professor of Horticulture. The title of Head of the Department of Botany was given to Professor William A. Kellerman. The building in which the classes in botany were conducted at that time is described in the catalogue of the university as follows:

> Botanical Hall was provided in 1883 by a state appropriation of fifteen thousand dollars. It is of brick and fifty feet long by forty feet wide. The whole structure is two stories in height. The general Botanical Laboratory occupies the second floor of Botanical Hall. It is 23x33 feet and is furnished with both movable and fixed tables. The latter are attached to the west and south walls near windows suitably shaded. Water, gas, and an evaporating hood are provided. The laboratory is equipped with compound microscopes of the Bausch-Lomb, the Leitz, and other patterns and accompanying each is a tray of tools and a case of reagents. There are more than fifty dissecting microscopes, also charts and several minor pieces of apparatus for experiments in vegetable physiology. Three smaller rooms are also provided as laboratories for special work as well as a dark room for photography. Other facilities for the illustration of the courses in botany and for practical training in the same are: a general herbarium including flowering plants, ferns, mosses, fungi, algae, a State Herbarium, a collection of fruits and seeds, valuable timbers, woods, grasses and various economic products of the vegetable kingdom; ornamental grounds and woodlands planted with a large variety of evergreen and deciduous trees and shrubs and a greenhouse with a fair collection of native and exotic plants.[3]

It should be said for the defense of this meager collection and the limited space that housed it, as we now may regard it, that it was representative of the conditions of the struggling state universities throughout the country. Only a few institutions were better equipped. In 1897, five years after Professor Kellerman had arrived, he listed in the department three herbaria, the general one, the state herbarium, and his own private herbarium of over 20,000 specimens. It had taken much effort and money to obtain these, and they were "deposited for use in the Botanical Dept."[4] In addition he had added a complete collection of native Ohio woods and a collection of native medicinal plants. But it should be said that botany as a science was beginning to emerge from the stage of concerning itself exclusively with description. It was turning to the dynamcis of plant life. Dr. Kellerman was one of the earliest to be aware that physiology needed to be studied and taught. He introduced a course in physiology and the text used was the best American volume of the day, written by Dr. Charles Barnes. Among other innovations this book included the term photosynthesis to replace the words "carbon assimilation" used by previous writers. In teaching the plant physiology Dr. Kellerman is said to have wandered

[3]Ohio State University Catalog 1893.

[4]Ohio State University Catalog 1897.

far from his subject during a lecture hour. He would touch on main points but would leave to his assistants the job of quizzing. With the limited equipment, the amount of solid laboratory experimentation remains highly speculative. This may have developed ingenuity as well as put a severe tax on the patience of the assistant.

From Cope's *History of Ohio State University* is the statement that in 1898 Townshend Hall was completed.

> No pains or expense had been spared to make the building complete and satisfactory in every respect, and it was at that time the finest building of the kind in the country. It at once became an object of pride and admiration to the farmers of the state and did much toward awakening their interest in agricultural education and in reconciling them to the university.

Townshend Hall was formally dedicated by President Canfield, Dean Hunt, and the Secretary of the Board of Trustees, Mr. Cope. Townshend Hall was the first building of the Neil Avenue group. It flanked University Hall and Engineering. Across the oval were Botanical Hall and Orton Hall, which housed the university library as well as the geology department. From High Street there were only the President's Home, the Armory, and Hayes Hall. Except for residences of faculty members, the rest of the campus was without buildings. The woodlot at the northeast corner still contained remnants of the original beech forest. The campus served as a local flora collecting ground. Legend has it that the showy orchid inhabited the banks of the small brook that divided the campus. Perennially Professor Lazenby was asked to landscape the campus, but no funds except for tree-pruning seem to have been available. Two or three abortive attempts to start an arboretum or at least a garden were foredoomed to failure as the demands for buildings and roadways grew.

Botany, however, did not stem from the local situation. The department somehow became a center of learning, toward which students were attracted, and all Ohio was its collecting ground. Professor Kellerman was soon to collect farther afield. He began in 1902 his series of visits to Central America to study tropical fungi; his records of types new to science became so numerous that he established the *Journal of Mycology* to serve for himself and for others as a medium of publication of the discoveries. While he was away the main teaching duties fell upon Schaffner. The University Catalog lists fourteen courses offered during the school year. Some of these were for students in the Arts College and some for the medical and pharmacy students, since at that time the applications of botanical science to medicine and pharmacy were still regarded as more significant than the applications to agriculture. The field of plant physiology was still largely unorganized, though Schaffner taught plant physiology with the slight equipment that the laboratory afforded. The entire university enrollment for the year 1898–99 was 1,149 students. Some of the contemporary members of the faculty included: Edward Orton, Professor of Geology and State Geologist, who had "retired" from the presidency of the university in

1881 to go back to his beloved science; Sidney Norton, in chemistry; Samuel Derby, in Latin; William Rane Lazenby, in horticulture and forestry; George W. Knight, in history, political science, and constitutional law; David S. Kellicott, in zoology and entomology, and Albert M. Bleile, in anatomy and physiology. Some of the young men of the faculty included Wilbur Seibert, Francis Caldwell, Embury Hitchcock, William McPherson, Joseph Russel Taylor, Charles B. Morrey, Clair Dye, Thomas French, Charles Bruce, John Bownocker, Francis Landacre, William L. Evans, C. E. Sherman, Charles Foulk, and William L. Graves. John F. Cunningham was appointed Fellow and laboratory assistant in horticulture and forestry at this time.

The improvement of teaching and research was to become a single unified objective for Schaffner. The slim equipment was to be fully used. More would come. The collections necessary for a knowledge of the plant life of the state were to be increased. The various branches of botany were all to be explored. His papers reported studies in widely separated fields of the botanical sciences. In ecology appeared a paper on the origin of timber belts and on the spread of buffalo grass. These papers, forgotten now, contain subject matter again of interest to conservation programs. Their suggestive value was forty years ahead of their time. In plant physiology he wrote about self-pruning of trees, nutation of sunflowers, maximum height of plants. On the subject of weeds, already becoming prominent causes of loss to farmers and adding millions of dollars annually to operating costs of farms, he described the peculiar method of seed dispersal in tumbleweeds. To algology he contributed a paper in 1902 on Kansas desmids. These were pioneer works on little-known matters. They were serving to enlarge the mind of the young investigator and teacher and to prepare the way for those who would later specialize in these several fields. General botany was beginning to delve into the mazes of the fundamentals of plant life. If Professor Kellerman's lectures possessed breadth and were given in an interesting fashion, young Schaffner's work would attempt to plumb the depths and provide the lectures with new perspectives. He wanted to know how plants live, more than he cared about their existence as objects to be described. He was beginning the expansion of not only his own mental equipment, but his insight into the plant knigdom was also being utilized by the head of the department and others. There were too many courses offered by the small staff. The Catalog for 1902–1903 lists twenty-seven undergraduate and six graduate courses. The general herbarium had grown to 30,000 specimens, and Professor Kellerman's was still kept as a separate collection. Schaffner had found time to do all of this departmental work by unremitting effort, in which he did not spare himself. But he wanted more consolidation of effort

The Biological Club offered both a social outlet and a means of consolidating effort. It was later to become the parent of the Ohio Academy of Science and of at least two national honorary societies with biology as the major interest. At the November sixth meeting in 1899 Schaffner was elected president of the Biology Club. Taking his duties seriously he presented a paper at the following meeting December fourth entitled "The higher Phagophytes of Ohio." In December he

went to the Cleveland meeting of the Academy and read two papers. He was elected a trustee and a member of the publication committee. At the meeting of June 4, 1900, of the Biology Club, he was elected Editor of the Ohio State University *Naturalist*. This became, with its name altered to the *Ohio Naturalist*, the official organ of publication for the Ohio Academy, and in 1916 had its name again changed to the *Ohio Journal of Science*. Professor Schaffner remained Editor through all its changes and expansions from 1900 to 1918. Professor Hine was associate editor and Professor Landacre business manager through a number of years.

From a diary in possession of Mrs. Schaffner the following entries are quoted:

"Nov. 28, 1901. Thanksgiving Day. We entertained Prof. W. C. Mills and family for dinner. In the afternoon I went with Mills to the O. S. U.–Kenyon football game. For supper we entertained John Bridwell, Frederick Tyler and Otto Jennings and brother."

"Nov. 29. Meeting of the Ohio Academy of Science. I read two papers entitled, "The self-pruning of woody plants" and "Plant ecology of Ohio; a general outline," the latter in connection with Mr. Tyler."

"Nov. 30. Meeting of the Academy. I read a short paper on "Observations on the origin of forest belts in Clay County, Kansas." In the afternoon I went to the meeting of the Columbus Horticultural Society." These entries along with the remarks of the preceding paragraphs indicate the zeal with which Assistant Professor Schaffner was executing his duties and carrying forward the enthusiasm for plant sciences he was developing at Ohio State.

The years 1906 to 1908 brought about many changes in the now well-established and growing Department of Botany at Ohio State. Professor Kellerman was devoting his attention more and more to his chosen life work. He was the editor and proprietor of the *Journal of Mycology* and in the habit of furnishing from his own pocket funds for publication if the subscription was not sufficient. He was preparing to add the *Mycological Bulletin* to his sheaf of duties. The herbaria were growing in importance and interest as many collections were added. Some of these were the collections of Central American fungi. The talk of a new building to replace the inadequate facilities for teaching and research had not brought about results, but they would come. Associate Professor Schaffner's salary was inadequately small, but he and Mrs. Schaffner both worked in the laboratory (on one salary), and he was beginning to save money for a trip abroad. Surely he deserved it. He had three score or so valuable papers published in different highly reputable journals, and the *Ohio Naturalist*, which he had edited from the beginning, was a definite success, largely through his efforts. There were graduate students, such as Gleason and York, making noteworthy progress and reputations for Ohio State. Gleason had gone to Illinois, York to the University of Texas, and Jennings to the Carnegie Museum at Pittsburgh. Schaffner seemed to have a way with the advanced students, especially when he was at work with them after class hours. He could talk to them freely then, and the new problems of a phylogenetic system of classification held their interest more than the routine

classroom lectures. The roof leaked whenever it rained, the rooms were cold on chilly evenings, but physical discomforts were not important if the work in botany was going forward.

In 1906 the first Mrs. Schaffner, the beloved Mabel, died. In the March number of the *Botanical Gazette* appeared a notable paper on chromosome reduction in *Lilium tigrinum*. This paper re-established Schaffner's conclusions on the relation between chromosomes and Mendelism that he had foreshadowed, though not completely stated, in 1897. In this 1906 paper he acknowledged his grateful indebtedness to Mabel, who had prepared the 200 serial slides that his studies had required. She had helped him toward the recognition that his earlier work should have had. The July news items of the *Gazette* briefly recorded her death after a short illness. The notice mentioned her ability as a botanist of promise.

Mabel Brockett Schaffner had been the constant ally of her husband. In addition to the preparation of the slides she had studied the embryology of Shepherd's Purse and paved the way for Schaffner's publication of the first complete account of the embryology of a seed plant. Diary entries for May 26–30, 1906, indicate that on his return from the funeral in Kansas he had stayed at the home of his friends the Mills', had visited Professor and Mrs. McCall, and on the thirtieth contains the following: "worked at Mabel's drawings. They are nearly done, only some dotting in one. She was so anxious to get them done. They are on Bursa, Shepherd's Purse." Schaffner would bury his grief in his work. There were many problems he wanted to talk over with others. He would ask for a leave of absence and complete his work for his Doctorate. But where and how and who would carry on? Dr. Kellerman was interested in Central America and his trips put the teaching burdens on Schaffner. This was undoubtedly the most trying period—the most confused and confusing. It is not difficult to foresee what would happen to a shy, affectionate and lonely man.

At church he met Mrs. Mary Morton Sample and in April, 1907, became engaged to her. She was the mother by a former marriage of a daughter Jean and the courtship as recorded in diary entries indicate that Schaffner was reviving from his despair and even becoming gay. He went to the theatre to see Maude Adams in Peter Pan, took Miss Jean and Mary to the circus, attended church regularly, often twice in one day, and on May sixth, the first anniversary of Mabel's death, he and Mary shared with sympathetic tears the emotion roused by the Columbus Oratorio Society's performance of Haydn's "Creation."

Dr. Alfred Dachnowski—now Dr. A. P. Dachnowski-Stokes—was asked to fill Schaffner's place and especially to teach plant physiology during the leave for the school year 1907–1908. Dr. Kellerman would forego his contemplated fourth journey to Guatemala to study and collect tropical fungi. Schaffner was reappointed associate professor at a salary of $1600 a year. On this and with his savings and perhaps some income from his share of the Kansas farm he would go abroad. He could live on very little.

In a letter from Professor Daniel C. Schaffner there is the following statement: "When John went to Europe for graduate work his inten-

tion was to study at Berlin or at one of the other great German universities. However, he found no one there interested in or more than even incidentally conversant with the problems that were uppermost in his mind at that time. Consequently he spent several months in study in Paris and the greater part of his year in Zurich. At both of these places he found men interested in scientific research as he understood it and spent the months in an atmosphere of friendly and stimulating surroundings."

Comparison of these statements with the diary shows disagreement of several points. Clearly, reading the diary shows the confusion in John Schaffner's mind at this period in his life. He was emotionally down and up in rapid successsion. His work in the department was beginning to count with both his students and his colleagues. He had been editing the *Naturalist* for seven years and teaching botanical sciences for ten. He was forty-one years old and his experiences had matured him. After his return from travel and study abroad he would be capable of developing the fullness of his powers. Perhaps he could find the answers to his problems. He was distinctly turning toward problems of classification and had published four papers on the subject by this time. The great exponent of taxonomy in Germany was Engler, and it may be that Schaffner thought and spoke of systematic botany and the physogenetic systems he was beginning to develop. But he would not have found Engler receptive to views from an unknown American who probably would stir up discord in the views Engler was proposing. The most he could hope for from Engler would be to add one more monograph to the already extensive series. But this was not what was in Schaffner's mind. He was not finding fault with detail in an existing plan of study. He was trying to establish his own grasp on the plant kingdom as a whole. Anyway, there is no record in the diary of what his exact views might be. He did not, however, have Germany as a main objective. He sailed from Philadelphia to Liverpool, August 17, visited Oxford and Stratford. He spent a few days in London, staying at 21 Montague St., spent a few days in Paris and arrived in Geneva on September 8. He matriculated in the University of Zurich on October 14. Here he found a group of co-workers who accepted him and made him welcome. His diary once more records some of his experiences. He visited a Russian student affair, the Zurich Botanical Society, went to concerts in the Ton-balle, gave a talk in German at the Botanical Society, and entered fully into a delightful and lively gathering of intellectual comradeship. He only crossed Germany at the end of his stay on his way to Bremen to the ship for America. He had enjoyed his period of study in Zurich and made a warm friend and life long correspondent of Dr. Hans Schinz.

But a curious thing happened in Columbus. Kellerman had an opportunity to go away that was too fine to be resisted. The Board of Trustees of Ohio State University had caught the spirit of the investigations that were attracting Dr. Kellerman and some of his graduate students. Plant life was to be studied where it grew. The Ohio State University campus was to extend to Central America. The following quotation is from a notice that appeared in *Science*, August 23, 1907:

A TROPICAL SCHOOL OF BOTANY

> Professor Doctor Kellerman of the Ohio State University, Columbus, Ohio, has planned a tropical school of botany for next winter which ought to attract the attention of some of our young men who are fitting themselves for their life work as teachers of botany. The session extends from December 19 to March 19, and will be held in Guatemala, Central America. The campus will be located at Zacapa, 100 miles from the coast, Los Amates, 40 miles inland, Izabal, on Lake Izabal, and perhaps also at Livingston, on the coast. Only a small number of young men will be accepted, and those who intend joining are advised to do so at the earliest day possible. The fee for three months, including traveling expenses, board and lodging, is $226.00. The project is one that should be of interest to botanists generally, as affording excellent opportunities for instruction along unusual botanical lines.

There was Kellerman's dream come true. He had been there on collecting trips three times previously. He saw in a land of smoking volcanos and great differences in altitude many opportunities to study a great range of plant life in the field. He would take care of the fungi and the others could collect specimens in other groups of the plant kingdom. So far as I am aware, this is the first time any university in the United States had authorized a School of Tropical Botany. Guatemala was a good choice. The railroad was started on the Atlantic side, and the United Fruit Company had its banana boats organized with excellent schedules for the journey across the Gulf of Mexico. Field work in geology and archeology could be fitted into botanical operations. Our dependence upon the tropics for a number of valuable and interesting products was just in its infancy. This was the time to go.

Looking at the exciting possibilities of the newly authorized School of Tropical Botany, Dr. Kellerman's dream seemed to have swept him off his feet. He seems now to have forgotten his own and Schaffner's teaching schedules. Perhaps Schaffner's plans for a doctorate degree could be adjusted later. Kudos meant little to Schaffner anyway. As Dr. Kellerman prepared to leave for Guatemala in December, 1907, perhaps some such thought flashed through his mind. There is no record that he wrote to Schaffner, nor any mention in the diary that Schaffner kept that he knew at this time that Dr. Kellerman was leaving. Certainly, Miss Detmers and Dr. Dachnowski could not manage the overloaded teaching program unaided. President W. O. Thompson sent for Schaffner. This confusion meant that Schaffner never obtained his doctorate. Also, the School of Tropical Botany had its first and last authorized journey.

Dr. Kellerman did not return. He died, presumably of malarial fever, March, 1908, and was buried in Zacapa. Three years later Professor Schaffner was appointed his successor as head of the department. On board the Kaiser Wilhelm der Grosse in Bremen, March 24, 1908, Schaffner received word of the death of Dr. Kellerman.

THE PRODUCTIVE YEARS

The growth of the University during the decade from 1910 to 1920 brought many changes. If the dedication of Townshend Hall in 1898 had helped "reconcile" the farmers, its expansion by 1910 and the outbreak of the war in 1914 put many unforeseen pressures upon faculty and student body. The department of botany under Professor Schaffner's chairmanship was provided with better space and facilities. In 1914, in Autumn, the present Botany and Zoology Building was opened for instruction. For the portion given over to botany there were some changes made that never suited Professor Schaffner. The west wings were each shortened about twenty feet and this curtailed the number of small research laboratories and instructors offices and scrapped plans for the elevator to the fourth floor where the enlarged herbarium was to be located. The building was given a high pitched roof and the spaces under the eaves were to contain dioramas, stilled life of animals and plants. Funds for these were never available, so the top floor was left largely unused during the first ten years the building was occupied. It was said at the time the building was opened in 1914 that the department would never be large enough to fill the available space. Within less than five years of the opening of classes in the new building the enrollment had reached a thousand. Many circumstances, including a new appreciation of the relation of botany to agriculture and horticulture as well as its pursuit as a basic science contributed to the enlarged demands placed by students on the staff. Professor Schaffner had built well. Not a building merely, but his views of botanical sciences were sound, as the contributions now so steadily flowing from his pen showed.

Again at a time when there were changes in the department and adjustments to be made, Professor Schaffner was occupied by personal emotional disturbances. Mary Morton Sample Schaffner died in September, 1914, and was buried in Washington, Pennsylvania. However, he attended the meeting of the American Association for the Advancement of Science in December with Professor W. G. Stover. At the meetings he served as a delegate to the Sigma Xi meeting and was elected to membership in the recently formed Botanical Society of America. In June, 1916, Professor Schaffner was married to Miss Cordelia Garber who became the mother of three children: Grace Odile, John, and James.

In 1918 the diary records "I resigned the headship of the Department of Botany and am now Professor of Botany doing mostly research work." This period from 1918 to the close of his life is the most productive. Here his researches and publications ripened to display the wisdom that those who knew him at this time learned to appreciate. His diary of that period no longer records in detail his publications or his strivings. He has begun to think about the effect of his writings on others—to sit back and plan with a greater sweep the advances of knowledge.

In the earlier years he may not have perceived that his efforts in consolidating the research in cytology and morphology would result in the life cycle studies being widely used by others. They were published in the *Ohio Naturalist* and his privately printed *Laboratory Outlines*.

From there they found their way to textbooks and have appeared in many places from 1915 on through the years. The same may be said of the studies that proceeded from the embryology of Sheperd's Purse for which he always gave the credit of great help to Mabel Schaffner. All of botany was moving toward a better understanding of plants. Schaffner was no longer alone in his work as he had been when he started. And in the more intensified studies that developed in the twenties respectful recognition of the pioneering work of the early days of Schaffner was not lacking.

Perhaps the most satisfactory evidence of the soundness of Schaffner's views came in the field of taxonomy. The series, "The Classification of Plants," was begun in 1905 and continued until 1922. The series entitled "Principles of Taxonomy" ran from 1924 to 1931. In both series a total of twenty-two papers appeared in the twenty-six years. His studies were based on an examination of the fundamental structures of plants. Surely this topic was not new to botanists, yet in Schaffner's hands it began to yield amazing results. He seemed to have an almost uncanny ability to rearrange plant series that clarified the many evolutionary problems. From an entirely unrelated field of studies, namely the study of serum reactions, European workers, notably Mez and his co-workers, of the University of Breslau, proposed an evolutionary sequence which in its main features agreed with the Schaffner system. In passing rather briefly over this noteworthy contribution, since it is too loaded with a vocabulary and technical details to expand the subject here, one may say that the difference between Schaffner's treatment and the older works on taxonomy is the application of the newer knowledge of plants to a phylogenetic system. His insight into the developments of plants enabled him to go forward rapidly where others had been misled by the mazes of detail. As a young graduate student at Chicago he had accepted the Engler system enthusiastically as a great improvement. Later he found that a new era was initiated by Bessey's use of the Bentham and Hooker system in 1894. In 1905 Schaffner published an outline of the classification of plants. In 1910, in the second edition of his *Laboratory Outlines*, he included a "tree" of the sixteen phyletic groups. In 1928 his *Field Manual of the Flora of Ohio* followed his phylogenetic treatment consistently.

His statement of the fundamentals may be found in the following quotation from his "Phylogenetic Taxonomy of Plants."[5]

> Botanical science has at last advanced far enough that a rather conclusive taxonomy can be established on a true evolutionary basis. But in order to discern the taxonomic system of plants properly, so as to avoid reasoning from the particular to the general, the botanist must certainly be familiar with the general characteristics of the whole plant kingdom, have a knowledge of life cycles, and also must be somewhat acquainted with paleontology and with ecological relations. The principle of organic change along definite lines will then become profoundly evident.

[5]Quart. Rev. Biol. Vol. 9, p. 131.

From the broad canvas on which he painted the parade of the whole plant kingdom through the ages, he looked on at the struggles of the newly rising and dynamic subject of genetics. After his discovery of the behavior of chromosomes in *Lilium* that contained the basis for Mendelian heredity, the account of the relations was published by Sutton in 1902. Schaffner did not return to the subject in a publication until 1905, when he used the title that should have been employed in the *Lilium* paper, "The Nature of the Reduction Division and Related Phenomena." There were five papers intervening, and in 1910 appeared the paper, delivered when he had been president of the Ohio Academy of Science at its 1909 meeting. Its title was, "The Nature and Development of Sex in Plants." This subject occupied him more or less consistently for the rest of his career. More than any other single subject, it showed how definitely he maintained his position in controversy if he thought he was right. It is of fundamental interest to biologists to see how from the beginning Schaffner's non-Mendelian view of sex was close to being the correct view. There were in all, twenty papers published on the nature and determination of sex. In these he was mainly upholding his position that sex is an expression of a physiological state and must be viewed as male, female, and neuter and that it cannot be determined by the chromosome structure as in ordinary shifting Mendelian phenomena. Instead, the chromosome and its transfer was to be regarded as a manifestation of some larger control in the set-up of the complicated life processes of the cell.

It was only a step, but an important one, to pass from such a concept of sexuality to the experimentation in sex reversals. Here he found the way to demonstrate in many different plants that sex reversals could occur either in the presence or absence of the extra chromosome. In all there were sixteen papers on the subject of the control and reversal of sex. At the beginning of the series of publications most biologists were indifferent or actually hostile to the concept of non-Mendelian sexual phenomena. Toward the end he had many followers who saw in the idea of ecological control of sex the explanations of their own specialized fields of investigation. As a result of his endeavors, I for one, feel that Schaffner's work has broadened the researches in genetics to admit some of the concepts of physiology and ecology hitherto lacking. Again looking for a short statement which may serve to summarize Schaffner's position, I take the liberty to quote his words:

> Any attempt to seek an explanation of sexuality and sex in terms of a balance of genes instead of a balance of physiological states would be beside the mark, since in all of these processes the balance of genes apparently remains the same.[6]

This paper ends with the suggestion that the study of the principles of reversal as worked out in plants may throw some light on human cases as they occur in medical history.

The eleventh paper in the series on determinate evolution contains perhaps Professor Schaffner's only quotation from the Bible, although

[6]Bull. Torrey Bot. Club, Vol. 60, p. 96.

he was throughout his life a constant church member. He had completed a series of extreme evolutionary trends in plants and compares some of these to the human brain. He ends the paragraph with the remark quoted from Psalms: "I am fearfully and wonderfully made." Here is for Schaffner an expression of the intense curiosity that animated his long and useful career.

THE BIBLIOGRAPHY

The full citation of all of his papers follows. There is no other place, at present, where the entire list is to be found excepting this account. The Torrey Index has only about two-thirds of the full list.

It is hoped by this citation to show better than by the biographical sketch the full rounded activity of a truly great mind.

There were in all three hundred sixteen papers and books found in compiling the bibliography.[7] The following list presents them chronologically.

CHRONOLOGICAL CLASSIFICATION OF PAPERS

1894— 1	1918— 2
1895— 0	1919— 5
1896— 1	1920— 3
1897— 3	1921— 4
1898—10	1922— 5
1899—12	1923— 7
1900— 7	1924— 5
1901—13	1925—10
1902—17	1926—10
1903—22	1927— 9
1904— 8	1928— 8
1905—16	1929—10
1906—11	1930— 7
1907— 3	1931— 8
1908— 6	1932— 5
1909—10	1933— 6
1910— 9	1934— 5
1911— 3	1935— 5
1912— 8	1936— 4
1913— 4	1937— 5
1914— 7	1938— 7
1915— 7	1939— 4[8] (Unpublished)
1916— 2	—
1917— 2	316

The true significance of Professor Schaffner's contributions stands out if we attempt to classify the recorded writings. It is only then that

[7]Mr. Victor Greulach and Miss Ruth Krehl were of material aid in compiling the bibliography.

[8]Only the unpublished papers recorded in "Papers from the Dept. of Botany" by Prof. Schaffner are included here.

the wide grasp of the Plant Kingdom which was his becomes evident. The groupings are as follows:

CLASSIFICATION OF PAPERS BY SUBJECT

I. Systematic Botany (110)
  1. Taxonomy
    a. "Classification of Plants" series (1905–1922)....12
    b. "Principles of Plant Taxonomy" series (1924–1931)....10
    c. Studies of the genus *Equisetum* (1912–1938)....17
    d. Miscellaneous (1912–1938).... 6
  2. Floristics
    a. Catalogs, supplements and records of Ohio Plants (1900–1939)....49
    b. Keys and Manuals (Ohio and adjacent states) 1903–1931....13
    c. Lists of lower plants (Mostly for Kansas) 1901–1910.... 3

II. Evolution (15)
  1. "Studies in Determinate Evolution" series (1928–1938)....12
  2. Miscellaneous (1898–1938).... 3

III. Ecology (26)
  1. Prairie vegetation (1899–1926).... 3
  2. Ohio vegetation (1902–1914).... 3
  3. Kansas vegetation (1898–1907–1938).... 3
  4. Equisetum ecology (1928–1934).... 4
  5. Miscellaneous (1899–1930)....13

IV. Genetics (23)
  1. The nature and determination of sex (1910–1937)....20
  2. Mutations (1906–1925).... 3

V. Cytology (12)
  1. Studies related to genetics and reproduction (1896–1915).... 8
  2. Mitosis, etc. (1894–1908).... 4

VI. Physiology (36)
  1. Growth (1898–1905).... 7
  2. Self-pruning (1901–1909).... 5
  3. Rejuvenation (1926–1928).... 2
  4. The control and reversal of sex (1919–1936)....16
  5. Miscellaneous (1898–1932).... 6

VII. Morphology (38)
  1. Life cycles (1897–1906).... 8
  2. Floral structure and development (1897–1937).... 4
  3. Equisetum (1908–1938).... 7
  4. Miscellaneous (1901–1938)....19

VIII. Laboratory Procedure (41)
  1. Histological methods (1898–1900)....13
  2. Other laboratory methods (1900–1902).... 4
  3. Laboratory outlines and manuals (1902–1915)....24

IX. Miscellaneous (29)
  1. "News and Notes," etc. (1898–1915, 1935)....12
  2. Terminology (1902–1906).... 2
  3. Pathology (of Equisetum) 1931.... 1
  4. Zoology (1909–1923–1929).... 3
  5. Book reviews and reports....11[9]

[9]Not included in the total of 316.

LIST OF PAPERS ARRANGED IN THE GROUPS SHOWN ABOVE

I. Systematic Botany

1. Taxonomy

a. "Classification of Plants" series

The classification of plants, I. Ohio Nat. 5: 298–301. 1905.
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If we attempt to cast into form some of the outstanding achievements indicated by the long list of writings perhaps the following may serve:

1. Contains the first report for Botanical Science of the behavior of the chromosomes in the process of meiosis. This cytological advance embodied in the paper on *Lilium* in 1897 antedated by two or three years the rediscovery of Mendel's work.

2. The diagrammatic representation of life cycles now extensively used in text books first appeared in the published works of Professor Schaffner.

3. These papers contain the first complete series of illustrations of the embryology of a seed plant. As in the above case, these illustrations have been widely used in text books, or have been the suggestion for further research.

4. From morphological studies there developed a system of plant taxonomy differing from the widely used European systems but finding substantiation and agreement in the testing of natural relationships of serological methods.

5. Constantly upheld the stand that sex inheritance cannot be regarded for most organisms in the same light as simple Mendelian traits. In such organisms as possess a special chromosome associated with sex and in which sex reversal has not yet been shown to occur, Professor Schaffner took the position that sex is part of a physiological reaction system distinct from the Mendelian system.

6. Demonstrated experimentally principles of sex reversal. By the use of physiological and ecological methods Professor Schaffner was able to show that sex expression could be controlled. Vegetative divisions or "Siamese twins" cuold be developed as male or as female, in response to environmental conditions.

7. Through the examination of neutral states and the existence of inter-sexes in a wide range of forms in the plant kingdom, showed that only where the time of sex determination coincided with the reduction processes could sex expression appear to resemble superficially ordinary Mendelian expression.

8. Upheld the principle that all Mendelian inheritance is superimposed upon the fundamental inheritance in organisms.

9. Demonstrated the major evolutionary trends in the plant kingdom by an original system of comparative study.

10. Outlined the evolution of potentialities in the plant kingdom.

11. Became internationally recognized as an authority on the genus *Equisetum* and contributed numerous revisions to the interpretation of this group.

12. Since the subject of *Equisetum*, and the works on reproduction and sex reversal are of such paramount interest, a brief additional classification of these items is appended.

Special Classifications:

Equisetum.

1. Taxonomy	15
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Sex and Reproduction.

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MEMORABILIA

The passing of a great mind that has been an inspiration for others always brings recollections. We have shared a personality, we have momentarily apprehended a vision that is not ordinary. We build into a great picture only if we do not try to pretend that the subject of our thought was without weakness. From a number of letters from which the following statements are quoted the reader will find some of those endearing human traits not always perceptible in reviewing the accomplishments of a creative worker. I wish here to express my appreciation to the authors of the letters written to me, and to thank Mrs. Schaffner for the first one quoted. Not all letters received have been used, since the same thought was expressed by different writers.

WILLARD M. KIPLINGER, Washington, D. C.

"I remember the days when Professor Schaffner showed us that scum from the lake was full of marvels. I remember the classes in the old building which, they now tell me, is to be torn down. I remember the occasional gentle exasperation of Prof. Schaffner over the laggard understanding of the boys and girls that botany was a science, and not "just leaves." I remember our wide eyes when we were told that in some European universities Ohio State University in America was known merely as the location of Professor Schaffner. I remember when you and he were married. And now the years have passed and you have three children for which I am glad. And you have lost him, and we have lost him, and I'm sorry."

CHARLES J. CHAMBERLAIN, University of Chicago.

"Schaffner came to the University of Chicago in the autumn of 1896, attracted by the prestige of John Merle Coulter, who had become our first Head Professor of Botany. He was doubtless attracted also by the brilliant young palaeontologist, Dr. George Bauer, who had excellent material from the Galapagos Islands. He studied throughout the year with Bauer. His principal work, however, was in botany. Schaffner knew that most of Coulter's work had been of the "Gray's Manual" type of botany, but he also knew that Coulter was dissatisfied with the Rochester Code and was making the Engler and Prantl system, with its series of evolutionary lines, the basis for a more natural taxonomy.

This system, with a series of life histories, was the basis for the earlier courses in morphology at the University of Chicago.

Schaffner took the advanced morphology in Gymnosperms and Angiosperms. He also engaged in research in morphology throughout the year and published two papers which became classics, the life history of Sagittaria and the Macrospore Nucleus of *Lilium philadelphicum*.

On account of the unfortunate wording of the title of the *Lilium* paper, it was many years before Schaffner received the credit he deserved. In this paper he proved that Strasburger and Guignard, leaders in cytology of that day, were wrong in their claim that in the reduction of chromosomes in Angiosperms, there is a double longitudinal splitting. Schaffner described a transverse splitting at the second division. Later it was shown that Schaffner's transverse splitting was a separation of whole chromosomes. This, however, was comparatively unimportant, because Schaffner had proved a qualitative division in the Weissman sense instead of a quantitative division as Strasburger and Guignard claimed. Schaffner's figures show the situation as it is now seen with the most approved technique.

Schaffner was a profound thinker and an enthusiastic investigator, full of initiative, and he brought to our new department as much as he gained from it.

Schaffner and I became warm friends and, although technically I was instructor and he student, our relations were throughout those of colleagues.

He probably thought I was somewhat in advance, at least in taxonomy, but this was really not the case. For two seasons an undergraduate who had tramped the Chicago area for years with the Professor of Botany of the old University had

taken me with him to collect material for classes made up largely of high school teachers. He knew all the ferns, flowers, and shrubs, so that I already knew many of the plants of the dunes region which were new to Schaffner.

Schaffner came to the University of Chicago expecting to take the Ph. D. degree, but in the spring quarter he was called to Ohio State University.

Schaffner and I have kept in contact with each other, and I regard him as one of the foremost botanists our country has ever produced."

H. A. Gleason, New York Botanical Gardens.

"I was 22 years old when I applied and received a fellowship at Ohio State University. Having lived in the college town where I received my undergraduate training, it was also my first year away from home. For this reason, as well as my age, I was in a rather receptive mood and I had not been at Ohio State very long before I began to profit by my contact with Schaffner. Officially, I had nothing to do with him. I was assistant to Kellerman; as such I had charge of the herbarium, helped Kellerman in one or two of his classes, and during the first term registered for work under him in the graduate school. From this work I learned nothing, nor did I absorb much more from the minor courses which I took outside the Department of Botany. As a result, I did little or no class work during the second term, and had not registered at all during the third term.

I must have become acquainted with Schaffner very shortly after my arrival in Columbus. He was then a tall and very bashful man in his thirties. He occupied the very poorly equipped laboratories on the second floor of the old botany building, consisting, as I recall them, of one room of about 15x30 and another about 15x15. I do not remember whether he had an office of his own, or not. In the larger room were a few tables and a long table built against the wall, extending one full side and across one end. Here his handful of students sat on stools to carry on their laboratory work which was mostly morphological in nature. From time to time, I used to listen to his lectures. These were delivered to the floor, not to the students, in a sort of rambling, drawling monotone. I do not think his students, sophomores and juniors mostly, got much instruction or inspiration from them.

Schaffner and several of the graduate students were inveterate workers. I arrived at the building every morning at 7:45, and, except for two intervals for meals, kept steadily at it until eleven in the evening. Schaffner was always there late in the afternoon, and very frequently back again at night. Then with none of the formality of the classroom, we had dozens of interesting discussions, all of Schaffner's bashfulness and diffidence was forgotten and the arguments swept back and forth from one to the other until it was time to go home and to bed. Our discussions were mostly on evolution and phylogeny and Schaffner was loaded to the brim with ideas on both. Today, I do not remember a single point which was brought out in any of these numerous discussions, but I can say that the importance of phylogeny was so firmly impressed upon my mind that it was never forgotten, and that as a result I have consistently ever since attempted to introduce phylogenetic ideas into all of my taxonomic research.

The first Mrs. Schaffner was then alive. I must have seen her several times; I remember nothing about her activities or interests. I picture her now as a comparatively small but plump woman with a round rather attractive face and black hair, smoothly brushed down. It seems to me also that Schaffner addressed her as Mabel.

The graduate students at that time, if this will be of any interest to you, included Lumina Riddle, Clara Mark, Mabel MacKinley, Caroline Cormack, Jim Macowen, H. H. York, and myself. There may have been a few others; if so, I have forgotten them. We used to have many good times together, to which Kellerman and Schaffner were sometimes invited, and which they always seemed to enjoy very greatly. I remember one of these on Hallowe'en in 1904, when the girls cooked an oyster supper in the laboratory with the two professors as our guests.

H. H. York, as you must know, is now Professor of Botany at the University of Pennsylvania and it is possible that he can give you some further light on Schaffner. I have no idea what has happened to the others."

B. W. WELLS, North Carolina.

"As my mind goes back to the Ohio State days and I view the scene with the long perspective of twenty-eight years, one of the few monadnock's rising sharply from the campus plain is the towering intellect of Professor Schaffner. It was this quality of intellectual vigor and the tremendous range of his knowledge which resulted from it, that made Professor Schaffner one of the greatest botanists of his time. To have studied under him was one of the special privileges of my life.

As an undergraduate I worked in the 'Old Botany Building' above the Spring. There in addition to the prosecution of his cytological and systematic researches which he energetically carried on with his teaching, he had another self-imposed duty and that was the protection of the museum from the rain. As regularly as the showers came Professor Schaffner would quickly distribute the nondescript collection of pans, knowing from long experience just where the worst leaks were located. Instead of allowing the disturbing influence of a disintegrating building to affect him, he compensated for the building's deficiencies and carried on—the work, his botanical study was above everything to him and he conveyed this enthusiasm to his students who sometimes needed it when they too suffered from the rain or cold.

Professor Schaffner was at his best in conversation with his students and associates. He was almost a spendthrift with his time when it came to helping his students to a deeper insight into the special fields in which he was interested. I profoundly realize now that many horizons are broader today simply because Professor Schaffner took me on some of his long excursions in the realm of scientific and philosophical biology

It is with greatest satisfaction that I record my profound appreciation of the personality and activities of one of the most virile and original thinkers, painstaking investigators and inspiring teachers who has appeared in the field of American Botanical Science."

ROBERT F. GRIGGS, George Washington University.

"John H. Schaffner was one of the two or three men who most influenced my development. Upon analysis of my debt to him as compared with that to others who took the trouble to give of themselves to a young boy, it becomes clear that he contributed more to my store of factual materials and more especially to the biological principles developed from those facts than did any other.

He had, it seems to me, two outstanding endowments. The first I have already suggested. His remarkable mind. The second would come under the head of heart.

He had none of those easy tricks of a good mixer which make it possible for a man really of mediocre caliber, of the cheer-leader type, to carry with him a noisy crowd of rotarians, and so Schaffner was short of what commonly goes by the name of 'personality.' But he had something far finer though it did not bring him so much in the way of promoting his own advancement.

I have seen him sit by the hour discussing philosophy and religion with some student who after being brought up in a narrowly orthodox home found himself all at sea in the free atmosphere of the university. Not a few of our alumni, who have lived the most valuable lives, owe their orientation to his clear vision of fundamental moral and religious issues and his willingness to help them over the difficult transition from juvenile to adult philosophy.

I have often wished I knew more of his early years. Growing up largely alone on the Kansas prairie he never had the training in dealing with people which would have made him a leader of men. But somewhere in that lonely farmhouse there must, I think, have been keen intellects which contributed a rich heritage, and trained the mind of the boy in no ordinary fashion. One thing that makes me think that at least one of his parents must have had an exceptional mind is the fact that his sister was for a long time consultant to the Wisconsin legislature, drafting laws and advising as to social and legal progress the world over—certainly a position which required a high order of intellectual discrimination.

Schaffner's mind had a most remarkable clarity, carrying him straight to correct conclusions regardless of authoritative opinion to the contrary. Perhaps the best illustration of this quality was his early discovery, before the turn of the century, that there was a true reducing division in the meiosis of plants. In those

days the dogma of the great German cytologist, Strasburger, ruled American laboratories to such an extent that they could see only what Strasburger had found. Strasburger held that the reduction division consisted of two equational splits of the chromosomes, so that any differential sorting out of chromatin material between the daughter cells was impossible. Schaffner, studying his slides saw a true reduction division, insisted on it, and would not recant. But his professors would not let him publish his results and he was not sufficiently pugnacious to fight the matter through to a successful issue. A year or two later Mendel's law was rediscovered, it became clear that a true reduction was required to explain the facts of alternative inheritance. Then everybody could see what he had found and reducing divisions were described from every laboratory.

If Schaffner could have dominated authority and compelled the publication of his findings, he would have become the leader in the new cytology which developed our present far flung chromosome theory of heredity."

FIRMAN E. BEAR, Rutgers, New Jersey.

"Professor Schaffner was an embodiment of the best in a man of science. His vast store of knowledge in his field made him so humble that folks passed him by without realizing who he was, or what he stood for. I am glad to have been numbered among his students and friends."

L. E. MELCHERS.

"The passing of Prof. John Henry Schaffner brought definite memories of him and Ohio State back to me.

The opportunity to have had worked with a man of his character and ability is an enviable experience. Why, as a student, was I drawn to Prof. Schaffner and what did I admire about him?

I admired his modest, unassuming, unselfish manner; characteristic of his everyday life. He never was too busy with his own research and interests to assist students and seemed especially patient in helping someone who could not comprehend some point in botany. I still can see him explaining a point to some student, spending hours, first from one approach then from another angle.

I remember Professor Schaffner best in the environment of the 'old botany building,' where I studied botany at Ohio State. He created an atmosphere which I enjoyed. The old, inadequate, under-equipped botany building, long ago a thing of the past,[10] was my choice of places on the campus—it wasn't the building that counted—there was my teacher who was a master of numerous fields of botany. I loved his enthusiasm, his sense of humor, his contagious chuckle, for he always could see a funny side of things. The loyalty to his host of friends and his helpfulness to a fellow in trouble was well known. Little did I dream that I would locate in the state most often mentioned by him—Kansas. He inspired me to seek the truth, to be alert and accurate in my observations, and certain of my conclusions.

I shall not review his scientific contributions, but I wish to mention one of the many, which is outstanding; his work on the 'nature and control of sex.' John H. Schaffner in the botanical world is a famous name. Well may Ohio State be proud of having had on its roll such a faculty member. It is a cherished memory to have studied with this teacher and to have had him as my friend."

A. B. STOUT, New York Botanical Gardens.

"There are nearly fifty reprints in my files that bear the name 'John H. Schaffner' and several of these have the handwritten notation 'With the author's regards.' Most of these publications deal with the phenomena of sex in plants. They emphasize the physiological and developmental aspects of sex expression. They survey in a very comprehensive way sex behavior in the entire plant kingdom. There are extensive observations of the actual conditions and there are numerous important results of experimental studies, especially on the influence of

[10]This building was turned over to the State Department of Health when the present Botany and Zoology Building was completed in 1914.

environmental factors on the expression of sex. To me these papers have, through these various years, brought much of inspiration and I for one am glad to record my indebtedness to the work and the writings of John H. Schaffner."

CHAS. C. DEAM, Bluffton, Indiana.

"My personal acquaintance with Professor Schaffner began at an annual meeting of the A. A. A. S. about 30 years ago. He religiously attended the meetings of the American Association of Science and I met him almost annually at them. I associated with him at these meetings more than with anyone else. I found him always the same congenial fellow. His habits were exemplary. His life from boyhood to the end was one of simplicity. His deportment, language, and his writings all follow this law of simplicity. His writings evince a vast store of fundamental knowledge which he used to work out his theory of plant evolution. This achievement will always remain as a monument to his industry, research, and logical study.

As a teacher he was unexcelled. I know two of his pupils who now hold the chair of botany, one in a college and one in a university, who told me of his ability and how they revered him. His hobby, a study of the Equisetaceae, made him the foremost authority on the genus Equisetum of North America. When discussing with him the Indiana Equiseta, I recall how well he knew our species in every detail. The achievements of Prof. Schaffner are surely enough to satisfy the aspirations of the most ambitious."